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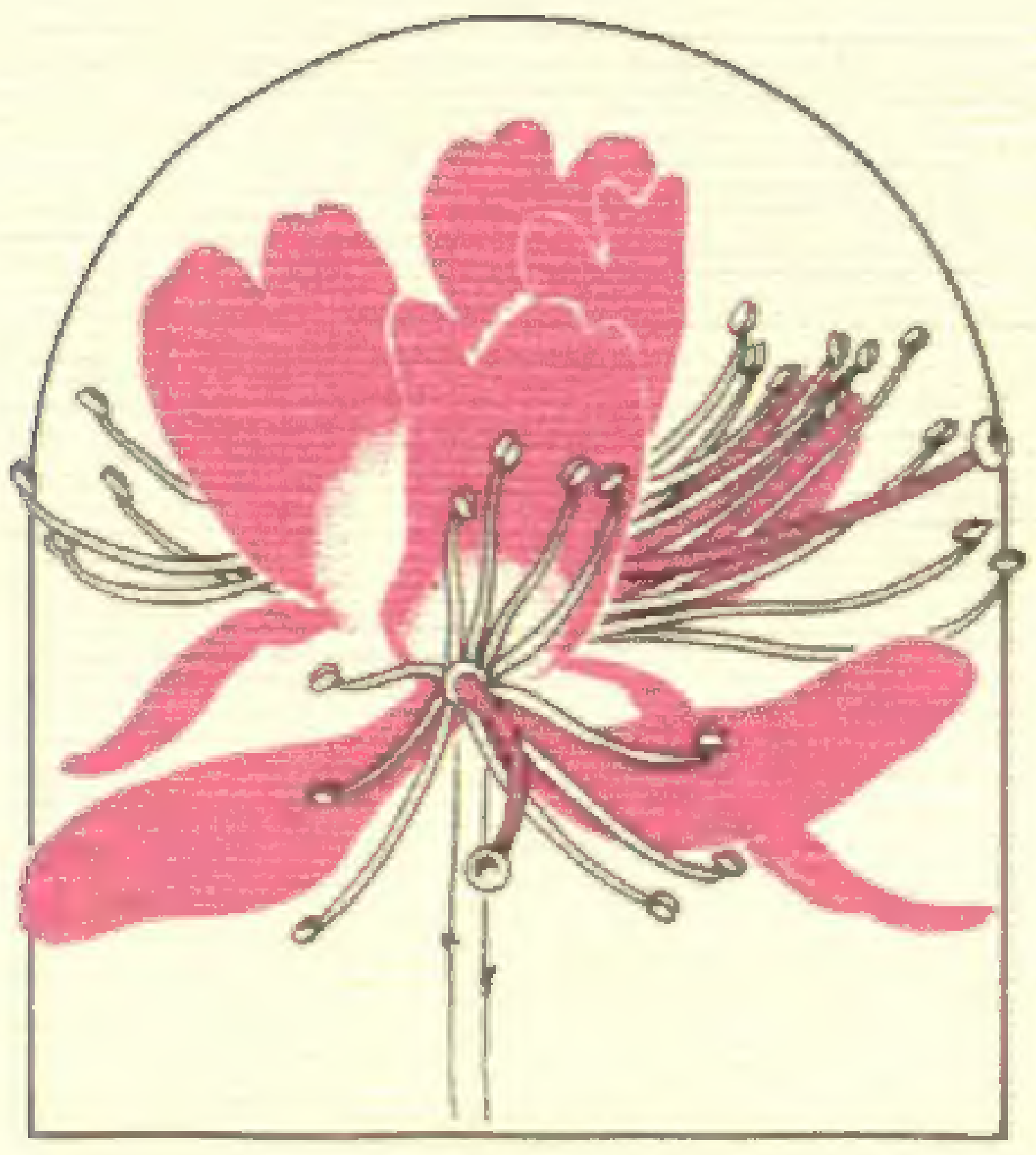

# RHODORA

## Journal of the New England Botanical Club

CONTENTS

Reflections on 100 years of *Rhodora*. *Janet R. Sullivan* .................... 1

A review of the taxonomic status of *Hackelia venusta* (Boraginaceae). *Richy J. Harrod, Lauri A. Malmquist,* and *Robert L. Carr* ............ 16

*Myriophyllum mattogrossense* (Haloragaceae), a rare lowland watermilfoil new to Bolivia. *Garrett E. Crow* and *Nur P. Ritter* .................... 28

Distribution and density of submerged aquatic vegetation beds in a Connecticut harbor. *Todd A. Randall, John K. Carlson,* and *Matthew E. Mroczka* ........................................ 40

The distribution of the bryophytes and vascular plants within Little Dollar Lake peatland, Mackinac County, Michigan. *C. Eric Hellquist* and *Garrett E. Crow* ........................................ 46

NOTE

More molecular evidence for interspecific relationships in *Liquidambar* (Hamamelidaceae). *Jianhua Li* and *Michael J. Donoghue* .......... 87

BOOK REVIEW

The Savage Garden ........................................ 92

NEBC MEETING NEWS ........................................ 95

Information for Contributors ........................................ 101

NEBC Membership Form ........................................ 103

NEBC Officers and Council Members .......................... inside back cover

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# The New England Botanical Club, Inc.

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# RHODORA

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# REFLECTIONS ON 100 YEARS OF *RHODORA*

JANET R. SULLIVAN, Editor-in-Chief

One hundred years ago the New England Botanical Club began publication of its journal, *Rhodora* (volume 1, number 1 was published in January, 1899). The Editor-in-Chief was Benjamin Lincoln Robinson of Harvard University. He was assisted by Associate Editors Frank Shipley Collins, Merritt Lyndon Fernald, and Hollis Webster, and members of the Publication Committee, William Penn Rich and Edward Lothrop Rand. The first issue of the journal comprised 20 pages of text and two plates, and was distributed to approximately 600 subscribers who had paid $1.00 each for the year's 12 issues.

That first issue of *Rhodora* opened with an editorial announcement (Editorial 1899) outlining the purpose of the journal ("... with confidence that it will give new stimulus and render material aid to the study of our local flora.") and describing the types of articles to be published. The expectations seem modest but inclusive and are clearly stated: that "... special attention will be given to such plants as are newly recognized or imperfectly known within our limits, to the more precise determination of plant ranges, to brief revisions of groups in which specific and varietal limits require further definition, to corrections upon current manuals and local floras, to altitudinal distribution, plant associations, and ecological problems." It was the intention of the editors to consider all contributions dealing with the "... flowering plants, ferns, mosses, and thallophytes ..."; presumably they intended to include the gymnosperms, as well. The announcement also states that "A decided preference will be given to articles which embody some newly observed fact, tersely stated."

The contents of the first issue encompass the angiosperms, fungi, and algae, with short papers and notes on rattlesnake plantains (Fernald 1899), *Myosotis collina* (Williams 1899), *Sanicula* (Brainerd 1899), fringed gentian (Deane 1899), wild lettuce (Robinson 1899), *Matricaria discoidea* (Manning 1899), algae (Collins 1899a), and fleshy fungi (Webster 1899). It is interesting to note, in these days when we are so conscious of the importance of peer review and the avoidance of conflict of interest, that all four of the editorial staff members were contributors to this first issue! Like a club newsletter might, the issue includes a listing of new NEBC officers, reports of meetings of other botanical clubs in New England, and a request for subscribers to report on the occurrence of inland populations of halophytes. The final announcement in the issue is a sort of "coming attractions," describing articles promised for the early issues of *Rhodora* and making an appeal for the submission of announcements of local floras in preparation.

During the period of the celebration of the Club's centennial in 1996 I became intrigued by the events that had transpired so long ago, resulting in a club and a journal I had respected, admired, and enjoyed since starting my formal study of botany in college in the 1970s. The year of the Club's centennial was also my first year as Editor-in-Chief of *Rhodora*; by the end of this year I had a new appreciation of what is involved in the production of a scientific journal. What activities of the Club's members warranted such an undertaking? Why did the NEBC decide to publish what was then a monthly journal?

## INITIATING PUBLICATION OF A BOTANICAL JOURNAL

The New England Botanical Club was established in February of 1896 "for the promotion of social intercourse and the dissemination of local and general information among gentlemen interested in the flora of New England" (Minutes of the 3rd Club meeting, February 5, 1896). By December of that year the members judged that the endeavor had been successful: the "faithful workers in the cause of botany," having been isolated previously, were meeting monthly, except during the summer, to share conversation and information about the New England flora as well as about new research and developments of botanical and ecological interest worldwide. In addition, the members of the Club had been true to their goal of providing "an elaboration of the New England flora," by accumulating specimens for the Club's herbarium (now NEBC), and by stimulating interest among the membership to provide local floras and plant lists. At the annual meeting in December, 1896, it was stated that "A plan for consolidating the information thus secured will shortly be presented to you." It was apparently from this interest in the dissemination of information about the flora of New England that the idea of publishing a botanical journal evolved.

By the fall of 1897 (Minutes of the 8th Council meeting, October 22, 1897), Dr. B. L. Robinson announced that Mr. F. S. Collins " . . . had his marine algae in such shape as to be ready to submit his list to the members of the Club before incorporating it in the checklist of New England plants." There were several local floras already in existence when the Club was organized two winters earlier, and the members had begun accumulating plant lists to be incorporated into a checklist of New England plants. In May and June of that year, Robinson's Publication Committee had requested help from the members in accumulating information for a checklist, particularly with verifying specimens and literature accounts. The effort to put together a checklist not only increased the holdings of the Club's herbarium, but eventually led to the publication of *Rhodora* and the revision of *Gray's Manual of Botany.*

The announcement that F. S. Collins was close to being able to submit his list for distribution sparked " . . . an exhaustive examination of the various systems of multiplication of writing . . ." By vote, the Council approved " . . . that Dr. Robinson investigate the possibilities of getting original papers to be submitted to the Club, hektographed by an assistant and that Mr. Collins' list be hektographed for distribution as an experiment provided the rate of cost be satisfactory . . ." [The hektograph was a predecessor of the spirit duplicator. Invented during the 1870s, it used a stiff gelatin pad and an aniline dye ink to produce copies.]

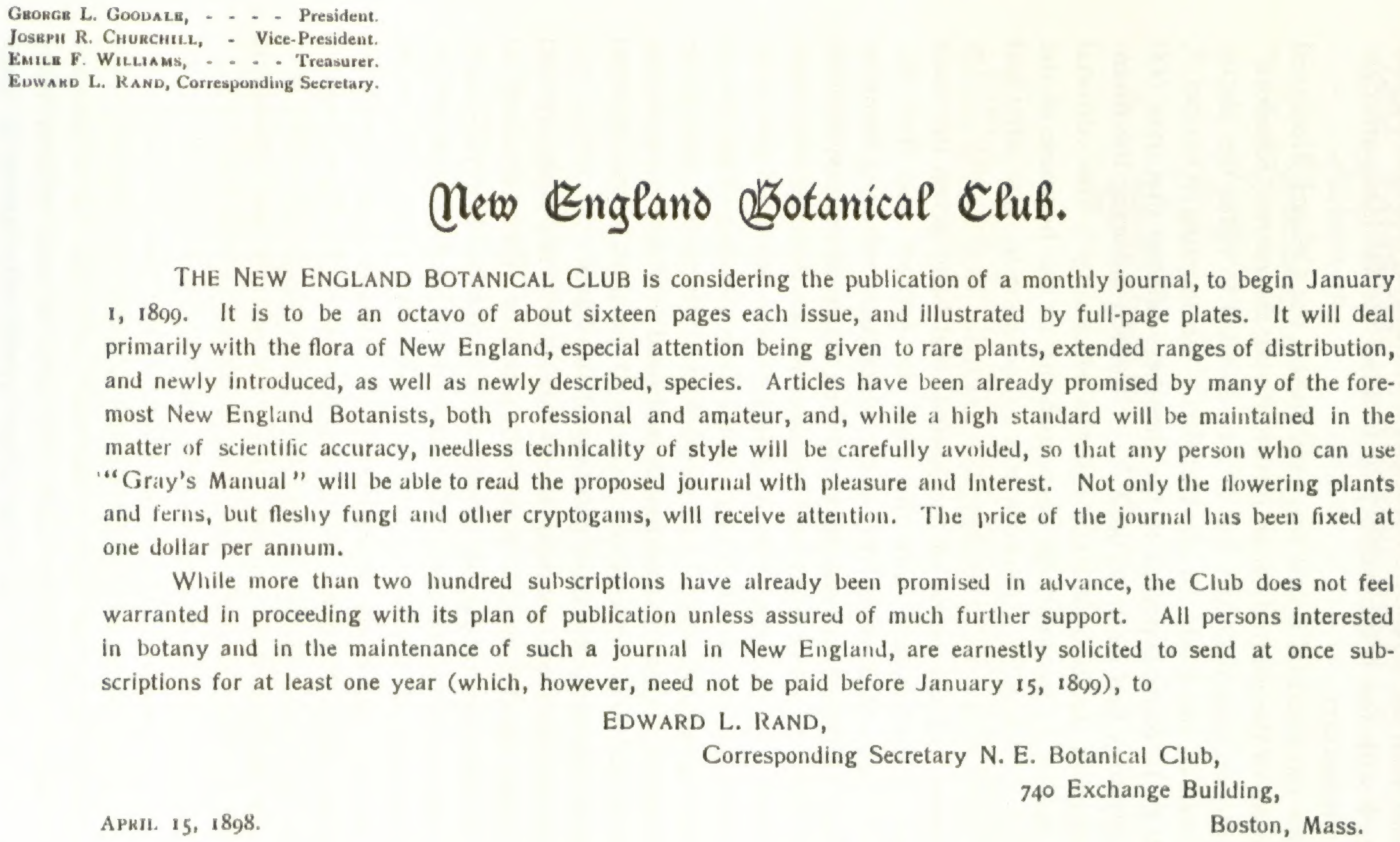
By February of 1898 (Minutes of the 10th Council meeting, February 21, 1898), the members of the Council were seriously discussing the publication of a " . . . Bulletin to publish botanical results arrived at by members of the Club and to become the organ of Descriptive Botany in New England." Dr. Robinson was ready to bring the matter before the Club in a formal proposal. The motion to appoint a committee to explore the possibility of producing a publication was carried unanimously at the Club meeting on March 4. At the next Council meeting (Minutes of the 12th Council meeting, March 23, 1898) Robinson presented an exhaustive report by the Publication Committee, and it was recommended that two members be appointed as a Financial Committee to investigate what support might be available for a serial publication. At the April meeting of the Club, E. L. Rand submitted a report by the committee which reviewed the different ways the publication could be supported, and recommended that not less than 400 subscriptions be obtained. The committee felt confident that the journal could be published without likelihood of failure with this number of subscriptions, and that "... any deficiency of income during the early stages could readily be met." Members of the Club present at the meeting exhibited a great deal of interest in the suggested publication.

In the Club scrapbook there is an unsigned, handwritten report dated "abt Mar 1898" which outlines the details of the journal recommended by the Publication Committee. It specifies a "... monthly issue of 16 pages and cover ... with illustrations to consist of six plates per year to be assigned free of charge to authors whose articles seem most in need of illustration ..." The report also notes the attributes desired of the first cover page, with "... the other three pages of cover to be used for advertising when appropriate and dignified advertisements are available." These advertisements were later to prove controversial, and soon were dropped from the journal.

The original proposal recommended that each author receive 25 free reprints of articles exceeding one page. The cost of the publication, including wrapping and mailing of 500 copies, was estimated to be $550.00 for the first year, although this was crossed out and $600.00 was penciled in above. The cost of an annual subscription was set at $1.00.

In April of 1898, a printed circular was distributed to the members of the Club announcing that the publication of a monthly journal was being considered, and requesting the assistance of Club members in obtaining subscriptions (Figure 1). The note accompanying the flier suggested that an average of 10 subscribers procured by each resident member (meaning members residing within 25 miles of Boston, where monthly meetings were held), and five by each nonresident member would assure the necessary financial support of the publication.

By the June meeting of the Council (Minutes of the 14th Council meeting, June 23, 1898), E. L. Rand reported that 450 subscriptions had been taken, and Robinson asked that the matter of organization of an editorial board be brought to a vote. The Council was in favor of immediate action and appointed B. L. Robinson as Editor-in-Chief, and F. S. Collins, M. L. Fernald, and Hollis Webster as Associate Editors. This editorial board, in con-



George L. Goodale, - - - - President.
Joseph R. Churchill, - Vice-President.
Emile F. Williams, - - - - Treasurer.
Edward L. Rand, Corresponding Secretary.

# New England Botanical Club.

THE NEW ENGLAND BOTANICAL CLUB is considering the publication of a monthly journal, to begin January 1, 1899. It is to be an octavo of about sixteen pages each issue, and illustrated by full-page plates. It will deal primarily with the flora of New England, especial attention being given to rare plants, extended ranges of distribution, and newly introduced, as well as newly described, species. Articles have been already promised by many of the foremost New England Botanists, both professional and amateur, and, while a high standard will be maintained in the matter of scientific accuracy, needless technicality of style will be carefully avoided, so that any person who can use "Gray's Manual" will be able to read the proposed journal with pleasure and interest. Not only the flowering plants and ferns, but fleshy fungi and other cryptogams, will receive attention. The price of the journal has been fixed at one dollar per annum.

While more than two hundred subscriptions have already been promised in advance, the Club does not feel warranted in proceeding with its plan of publication unless assured of much further support. All persons interested in botany and in the maintenance of such a journal in New England, are earnestly solicited to send at once subscriptions for at least one year (which, however, need not be paid before January 15, 1899), to

EDWARD L. RAND,
Corresponding Secretary N. E. Botanical Club,
740 Exchange Building,
Boston, Mass.

April 15, 1898.

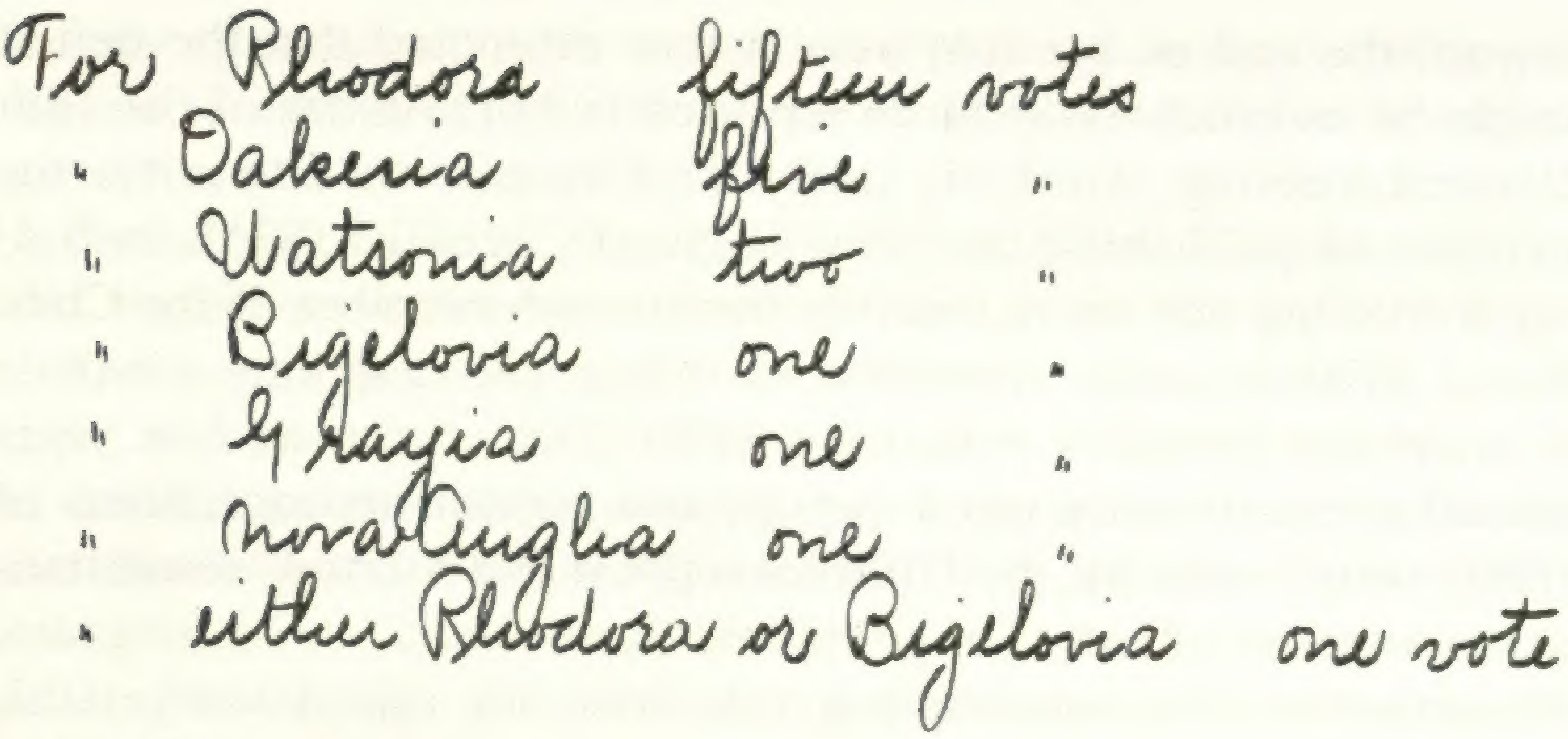
Figure 1. Copy of a flier announcing the New England Botanical Club's intention to begin publication of a monthly journal and soliciting subscriptions.

junction with the already established Publication Committee, was charged with the responsibility of making the business arrangements necessary.

Once the editorial board was established, the Council discussed the name of the journal; in an informal vote the name "Rhodora" was chosen unanimously, but it was decided to defer the matter to a vote of the Club. At the October Club meeting (October 7, 1898) E. L. Rand reported to the members present that over 600 subscriptions had been secured, ". . . thereby insuring the financial support deemed necessary for a beginning." The editorial staff had ". . . assumed the responsibility of the business of the journal . . ." and Dr. Robinson was called upon to state what had been done in regard to naming the journal. "In response . . . Dr. Robinson said the name of the journal had been given the most earnest consideration from the time the project was first discussed. He explained the very great advantages resulting from the use of a single name, not only as being more direct and definite in the minds of the botanical public, but as being vastly more convenient for the purposes of citation." He described the informal vote in favor of "Rhodora" at the June meeting of the Council, and there followed ". . . a good deal of discussion among the members in regard to the name proposed." There were strong opinions on both sides of the issue, and the matter was deferred for final action to the next meeting of the Club.

At the 27th Club meeting on November 4, 1898, the subject of a name for the journal was again taken up. There was a great deal of discussion, during which several names were proposed, and eventually an informal ballot was taken. Jesse Greenman was appointed by the Chair to collect the ballots and report the results (Figure 2). "Mr. Rich, seconded by Mr. Kidder, then moved that the Club adopt the name 'Rhodora, Journal of the New England Botanical Club,' as the official title of the proposed publication and the motion was carried with only one or two dissenting votes."

Thus the journal was underway, after a year of formal discussion and preparation. The Club ended its third year on a high and hopeful note; the members felt secure that the new journal would be self-sustaining, at least at the start, and that its publication ". . . would reach far and wide, not only our non-resident members . . . but also the great botanical world, who knows us not." In the summary statements closing the meeting, the new journal



For Rhodora fifteen votes
" Oakesia five "
" Watsonia two "
" Bigelovia one "
" Grayia one "
" nova Anglia one "
" either Rhodora or Bigelovia one vote

Figure 2. Tally of votes taken on the name of the new journal (from the Minutes of the 27th Club meeting, November 4, 1898).

was noted as the highlight of the Club's achievements: ". . . the Club now has a voice . . . It remains for the members to make that voice heard for the best interests of our favorite science and the result we hope will justify the establishment and maintenance of the Club. This is a momentous period for us and the prosperity and perhaps even the existence of the Club will depend upon the faithfulness with which each one contributes to the success of our undertaking. The labor we have undertaken is great, but as members of the New England Botanical Club, we should be untrue to our aims and ideals if we did not make the effort to attain them."

These powerful and encouraging words still ring true today; while the existence of the Club may not depend on the publication of the journal, both the existence and quality of the journal still depend primarily upon the contributions and dedication of Club members.

## PUBLISHING A BOTANICAL JOURNAL

The work had only just begun. The editorial staff and many other members of the Club spent the first year of the journal's publication encouraging the submission of manuscripts, soliciting new subscriptions, obtaining advertisements to help defray costs, and working to maintain the monthly publication schedule.

Publication costs were higher than originally anticipated, due to the decision to electrotype each page. In addition, the inclusion of an index had not been part of the original calculations, and toward the end of the first year it was estimated that the deficit might be as much as $200. In April of 1899 (Minutes of the 18th Council meeting, April 21, 1899) the Council voted to cover the expense of publishing the New England Checklist ($35), including providing one set of reprints free to each member of the Club. Emile Williams was appointed to obtain subscriptions adequate to meet the journal's deficit for 1899. Over the next few years *Rhodora* consistently ran a deficit, and regular appropriations of funds were made by the Club to support the journal, sometimes at the expense of increasing the holdings of the Club's herbarium. Nevertheless, the subscription rate was not raised until 1912, when the price of receiving the year's issues went from $1.00 to $1.50 per year.

In those early years, the journal carried advertisements to help defray the costs of publishing plates. Both W. P. Rich and E. L. Rand had addressed the Club, describing to the members the desirability of securing advertisements in order to enable the editors to increase the number of pages and to publish more and better plates. The earliest advertisements were for booksellers, collections of dried and live plant specimens, and the "Nurseryman's Directory." After the excursion to Mount Katahdin by five NEBC members in July 1900, an advertisement appeared offering "Katahdin on Horseback" (volume 3, 1901). The charge for a 4″ × 3/4″ space was quoted as $4.00 per year (volume 5, 1903).

The largest ads, running from one to four full pages, were purchased by the Bangor & Aroostook Railroad and offered rail passage to remote plant collecting sites. These ads immediately proved controversial, because they itemized locations of rare species in addition to offering safe, comfortable passage. An editorial published in volume 3 (Editorial 1901) defended the ads and the naming of rare species, stating that the plants in question were abundant at the sites to be visited, and adding that some of the species mentioned were considered weeds by farmers or were timber pests. The ads continued to be published during 1901, but the controversy led to diminishing numbers of ads of all kinds over the next few years and advertising was dropped from the journal by volume 9 (1907).

From a scientific standpoint, the Club's members were 'entirely satisfied' with their new journal. The early volumes of *Rhodora* were filled with short papers and notes outlining the distribution of particular species in the New England states, describing "noteworthy specimens" with unusual morphology, and providing additions to the checklist. One of the most quaint articles described the effects of an inadvertent *Boletus* poisoning at a brunch held at the home of one of the editors, F. S. Collins (Collins 1899b), and argued for better identification manuals for the region's flora.

The journal also featured short articles detailing meetings, field trips, and histories of other botanical clubs in New England, such as the Connecticut Valley Botanical Society, the Josselyn Botanical Society, the Vermont Botanical Club, and the Boston Mycological Club. Short book reviews and obituaries started appearing in volume 2, as well. Longer articles commemorating the lives of deceased Club members each featured a formal portrait and signature.

Volume 3 devoted a considerable number of pages to a diary kept of the botanical excursion to Mount Katahdin the year before by five members of the Club (Churchill 1901). The editors also allowed publication of seven plates accompanying this article. In addition, members of the party contributed four other articles on the botanical aspects of the trip (Collins 1901; Fernald 1901; Kennedy and Collins 1901; Williams 1901). This was the beginning of a tradition of publishing botanical commentaries on Gray Herbarium and New England Botanical Club expeditions.

Originally, the scientific articles published in *Rhodora* were mostly field observations, though the results of laboratory experiments and study of herbarium specimens started appearing in very early issues. Although notes of one or a few paragraphs continued to be a feature of the journal for many years, the length of articles and their scientific content increased significantly over the first few years of publication.

Nevertheless, manuscripts were difficult to come by in those early years. The members of the editorial staff were frequent contributors to the early issues; a glance at the index to volume 1 shows that Robinson wrote four articles and notes, Collins wrote five, Fernald wrote 15, and Webster wrote eight. The items contributed by the editors amounted to 28% of the total published that year; the percentage was almost as high for volume 2 (25%). This must have been a considerable burden for the editors; B. L. Robinson addressed the problem at a Club meeting, asking the members ". . . to bear in mind Rhodora which is much in want of copy . . ." (Minutes of the 45th Club meeting, October 5, 1900). After a few years the journal had a group of supporters who submitted articles regularly, and in 1929 it was noted that articles by 399 different botanists had been published in *Rhodora* (Editorial 1929). By the 1940s the number of pages published per year had increased considerably, as had the number of plates.

By far the most prolific contributor to the journal was Merritt Lyndon Fernald. An apparently tireless researcher, Fernald published an average of 13 articles and notes per year (range 4–25) from the time the journal was established until his death in 1950. He also served on the editorial board during this entire period, first as an Associate Editor (1899–1928) and then as Editor-in-Chief (1928–1950) after the resignation of B. L. Robinson. His contributions encompass the full spectrum of types of articles published in the journal during its first 52 years; commentaries on botanical expeditions, notes on the distribution of taxa, floristic and taxonomic treatments, descriptions of new species and varieties, details of anomalous plant distribution and morphology, and descriptions of new plant collecting techniques all can be found among the papers he wrote for *Rhodora.* One may wonder whether the journal could have survived the early paucity of manuscript submissions if it had not been for Fernald's contributions.

In addition to the variation in availability of publishable material, the journal suffered an inevitable fluctuation in subscriptions. As late as 1928 members of the NEBC Council were still struggling to improve circulation. Originally, having a subscription to *Rhodora* was not tied to membership in the Club. [It was not until 1968 that women were admitted to the NEBC as members, and not until 1996 that membership was automatic upon application.] It was expected after the first year of publication that there would be a "considerable falling off in subscriptions, many of the first year's subscribers finding it altogether above their interest and understanding." The list of original subscribers surely included some who fell into that category, but the subscription list also must have expanded beyond New England fairly early. At the end of the first year (volume 1, number 12), W. P. Rich called for a prompt renewal of subscriptions, listing the cost as "$1.00 per year for the United States and Canada, $1.25 for other countries." Manuscripts were contributed by botanists from outside of New England almost from the start; as early as volume 2 a note appeared by William M. Canby of Wilmington, Delaware (Canby 1900), and in volume 3 a note was published by Charles Bessey of the University of Nebraska (Bessey 1901).

In volume 21, F. S. Collins published the first article about plants occurring outside of North America (Collins 1919). Back issues were already scarce by volume 3, and a special notice published in 1901 encouraged interested readers to send the $1.50 necessary to secure a copy of the fast-disappearing issues of volume 1. "An early response will be necessary . . ." warned the editor.

In 1900 (volume 2) the journal fell behind in its publication schedule because of a fire at the printing office. "It appears that the entire April issue was destroyed, but as full sets of proofs had been printed and sent the issue will be immediately reprinted with a delay of perhaps three weeks." (Minutes of the 41st Club meeting, April 6, 1900). Luckily, the plates had been stored in a vault and were unharmed by the fire. The journal continued to appear on a monthly basis, more or less on schedule, until 1962 when publication was changed to a quarterly schedule. At this time the subscription rate was raised to $6.00 per year.

## *RHODORA* TODAY

In some ways the business of publishing a botanical research journal has not changed in the past 100 years, and in other ways it has changed dramatically. We still suffer fluctuations in suitable manuscript submissions and journal circulation, and we still need to maintain a regular publication schedule to satisfy both our subscribers and the U.S. Postal Service. Beyond that, however, the original editorial staff of the journal probably would be amazed at the changes in the complexities of the process. The papers published in *Rhodora* today involve more experimental results than pure description, reflecting that trend in botanical research over the past fifty years. The degree of specialization in research necessitates enlisting the help of reviewers beyond the editorial board. The papers published today are longer than those in the early issues of the journal, and typically include tables and figures. Likely, it has been the increased level of detail in manuscripts, combined with the use of word processors rather than secretaries, that has contributed to the workload and, thus, to the decreasing tenure of editors of *Rhodora* (Figure 3), despite the redistribution of some of the more tedious tasks among the press and editorial board members. Certainly, the authors and members of the Club and its council could not have been any more en-

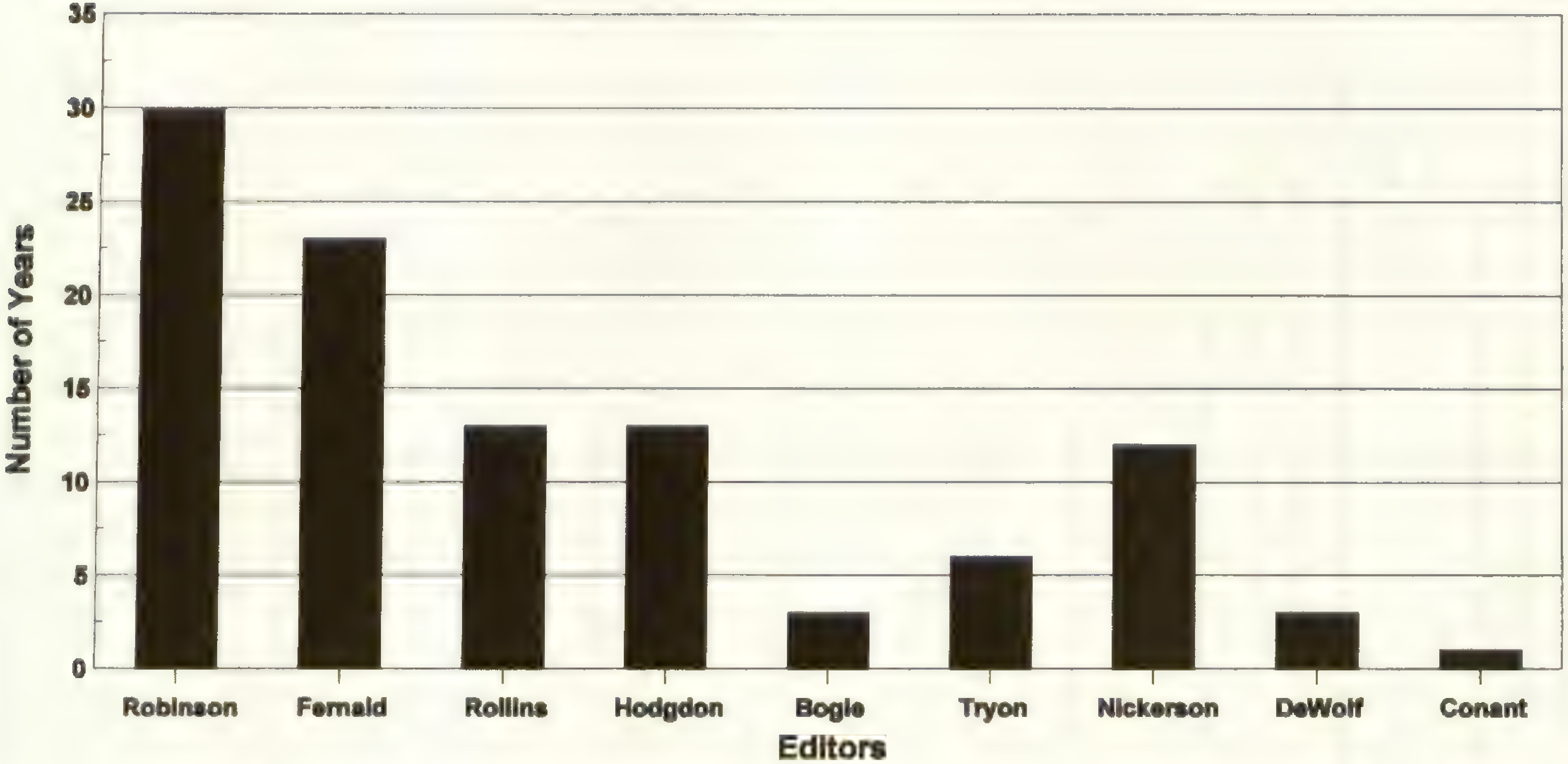


Figure 3. Illustration of the trend in decreasing tenure of Editors of *Rhodora*. When two Editor's terms overlap each has been rounded off to the full year.

couraging and supportive in the early years than they have been during my term thus far!

In addition to reflecting changes in the field of botany, *Rhodora* reflects the changes that have occurred in the membership of the New England Botanical Club. In its early years, the Club membership consisted of an approximately equal mixture of amateurs and professionals; in a 1995 survey 75% of the respondents listed themselves as students or professionals having employment related to botany. In addition, the early members of the Club were mostly "resident" members; that is, members who lived within 25 miles of Boston. By the time Fernald assumed the position of Editor-in-Chief, the journal boasted 33 Old World subscribers (Editorial 1929). Today the Club's membership and subscribers range worldwide, and manuscripts are regularly submitted from outside of the U.S. One of the regular features of the journal, NEBC Meeting News, attempts to keep distant members informed of the content of our monthly seminars.

When he took on the job of Editor-in-Chief, Fernald began his term by publishing an overview of the accomplishments of the journal's first 30 years (Editorial 1929). At that time, it was reasonable to relate such statistics as the number of new and total contributors per volume, and to name some of the more faithful contributors. Since then, many new, more specialized periodicals have begun publication, drawing papers away from the more general botanical journals such as *Rhodora.* Still, the journal has maintained publication of high quality papers on a variety of topics in botany. In addition, the elimination of page charges in 1996 has made publication in the journal more accessible to students and professionals with limited funds.

In his 1929 editorial announcement, Fernald took the opportunity to restate quite eloquently the parameters within which manuscripts should fit in order to be appropriate for publication in *Rhodora:* "The pages of *Rhodora* are not reserved . . . for members of the Club. They are freely open to all who care to use them, especially for the publication of tersely stated notes on range extensions or new or unrecorded facts regarding habits, morphology, habitats or other features of interest to students of all plants . . . or the natural history of plants. Systematic revisions and monographs of groups represented in the flora of northeastern North America will be welcomed for editorial consideration and well-written and descriptive (but not prolix) accounts of explorations, containing a good share of new or significant observations, will be gladly considered. Mere lists without clear statement of the significance of the records are less desirable. Illustrations of new species and of newly recognized diagnostic characters are most desirable . . . Photographs of landscapes, unless they are remarkably sharp and of patent significance to the discussion, are undesirable for reproduction and, in general, *Rhodora* cannot commit itself to publish them. . . . Manuscripts which show serious lack of consistency will necessarily be returned for correction. In case of misquotations, erroneous citations and other inaccurate details in manuscripts the editors will naturally make corrections of obvious errors. They cannot, however, be expected to specially check such matters and it will be inferred that authors have themselves verified such essential details. Neither can the editorial board be held responsible . . . for all statements and conclusions presented by different authors. In the case of controversial subjects, with the desire to present both sides of a question, papers may be accepted for publication, though not representing the views of the editors." While the possibilities may seem a bit limited by today's standards, Fernald could not have anticipated the full range of submissions, especially the range of experimental techniques, available to researchers 70 years later.

The details of the discussions 100 years ago on the name of the new journal were not recorded in full. We know that *Taxus* was suggested in jest, and we know the other, serious considerations that were included in the vote. Apparently, some members felt that the name "Rhodora" was "too sentimental," perhaps because of the poem by Ralph Waldo Emerson, although that connection has not been mentioned elsewhere. Apparently, some members with more limited vision felt that the name "Rhodora" would be appropriate for a club whose members had a primary interest in plants with the same range (Editorial 1929; Howard 1996; Pease 1951). Whatever the thoughts of those 26 voting members in 1898, *Rhodora* now serves readers worldwide and, while concentrating on the flora of North America, information on related taxa and comparable ecological phenomena from beyond that limit are considered for publication.

ACKNOWLEDGMENTS. I am indebted to the members of the New England Botanical Club, especially the Council members and ed-

itorial staff, who have provided so much encouragement and support during my three years as Editor.

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# A REVIEW OF THE TAXONOMIC STATUS OF *HACKELIA VENUSTA* (BORAGINACEAE)

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ABSTRACT. Morphological variables were analyzed using principal components and discriminant analyses to determine patterns of relationships among populations of *Hackelia venusta,* a narrow endemic, and *H. diffusa* var. *arida,* a relatively common species. The results of the analyses indicate that *H. venusta,* as currently circumscribed, consists of two discordant taxa with the population from the type locality at a low elevation clearly distinct from high elevation populations that have been assigned to this species. The high elevation populations represent an undescribed taxon. No affinities with either the low elevation *H. venusta* or the high elevation undescribed taxon were found to exist with populations of *H. diffusa* var. *arida.* Both *H. venusta* and the undescribed high elevation taxon are very narrow endemics and would benefit from well-developed conservation strategies and subsequent management.

Key Words: *Hackelia,* taxonomy, rare species

*Hackelia venusta* (Piper) St. John, showy stickseed, is a narrow endemic species of the Boraginaceae currently known only from Chelan County, Washington. As described by Gentry and Carr (1976), the species is a moderately stout perennial, 2–4 dm tall, often with numerous, erect to ascending stems from a rather slender taproot. It has large, white, showy flowers. The nutlets are 3–4.5 mm long, with 8–14 intramarginal prickles. The marginal prickles are fused for up to ½ their length, forming a flange ca. 1 mm wide. It is found on steep, rocky slopes covered with granitic scree.

The species was first described by Piper (1924) in the genus *Lappula* and was later transferred to *Hackelia* by St. John (1929). The original description given by Piper was based on a 1920 collection made by J.C. Otis (*895,* US) at a site about seven miles northwest of Leavenworth in Tumwater Canyon at an elevation of 488 meters. Piper described *H. venusta* as having a white corolla about 2 cm broad. In 1947, a specimen (*Long 14,* WS) was collected about 16 km south, southwest of the Otis collection in the Alpine Lakes Wilderness, Chelan County, at an elevation of 2030 meters. Subsequently, researchers (Carr 1974; Gentry and Carr 1976; Hitchcock et al. 1959) included this alpine collection in their circumscription of the species and noted that flowers are white or sometimes washed with blue. Since that time, three additional alpine populations assumed to be *H. venusta* have been located, one from an area near the Otis collection (*Harrod 238,* Leavenworth Ranger District Herbarium), one from Asgaard Pass (plants have not been relocated since 1995, Harrod unpubl. data) and the other from Cashmere Mountain, all above 2000 meters within the Alpine Lakes Wilderness area.

Some recent workers have suggested that the high elevation populations may be taxonomically distinct from the Tumwater Canyon *Hackelia venusta* (Gamon 1988; Loyal A. Mehrhoff, USFWS, Portland, OR, and Kathleen Robson, Robson Botanical Consultants, Vancouver, WA, pers. com.). The purpose of this study was to evaluate the relationship of these populations in order to achieve a better understanding of the taxonomic status of *H. venusta.* Because of the possibility of some allopatric introgression between *H. venusta* (*sensu stricto*) and populations of *H. diffusa* (Doug. ex Lehmann) Johnston var. *arida* (Piper) Carr in the lower end of Tumwater Canyon and several coulees north of Leavenworth (Carr 1974; Gentry and Carr 1976), a number of populations of the *H. diffusa* var. *arida* were included in the study.

## MATERIALS AND METHODS

**Study sites.** Data were collected from ten populations in Washington shown on the map in Figure 1. Collection sites for *Hackelia venusta* (*sensu lato*) were located on the Wenatchee National Forest in Tumwater Canyon (TC), 9.6 km west of Leavenworth, 488 meters; Crystal Creek (CC), 19.0 km southwest of Leavenworth, 2030 meters; and on Cashmere Mountain (CM), 16.0 km southwest of Leavenworth, 2073 meters. Collection sites for *Hackelia diffusa* var. *arida* were located on the Wenatchee National Forest in Tumwater Canyon (TW), 1.6 km west of Leavenworth, 400 meters; Derby Canyon (DE), 11.3 km southeast of

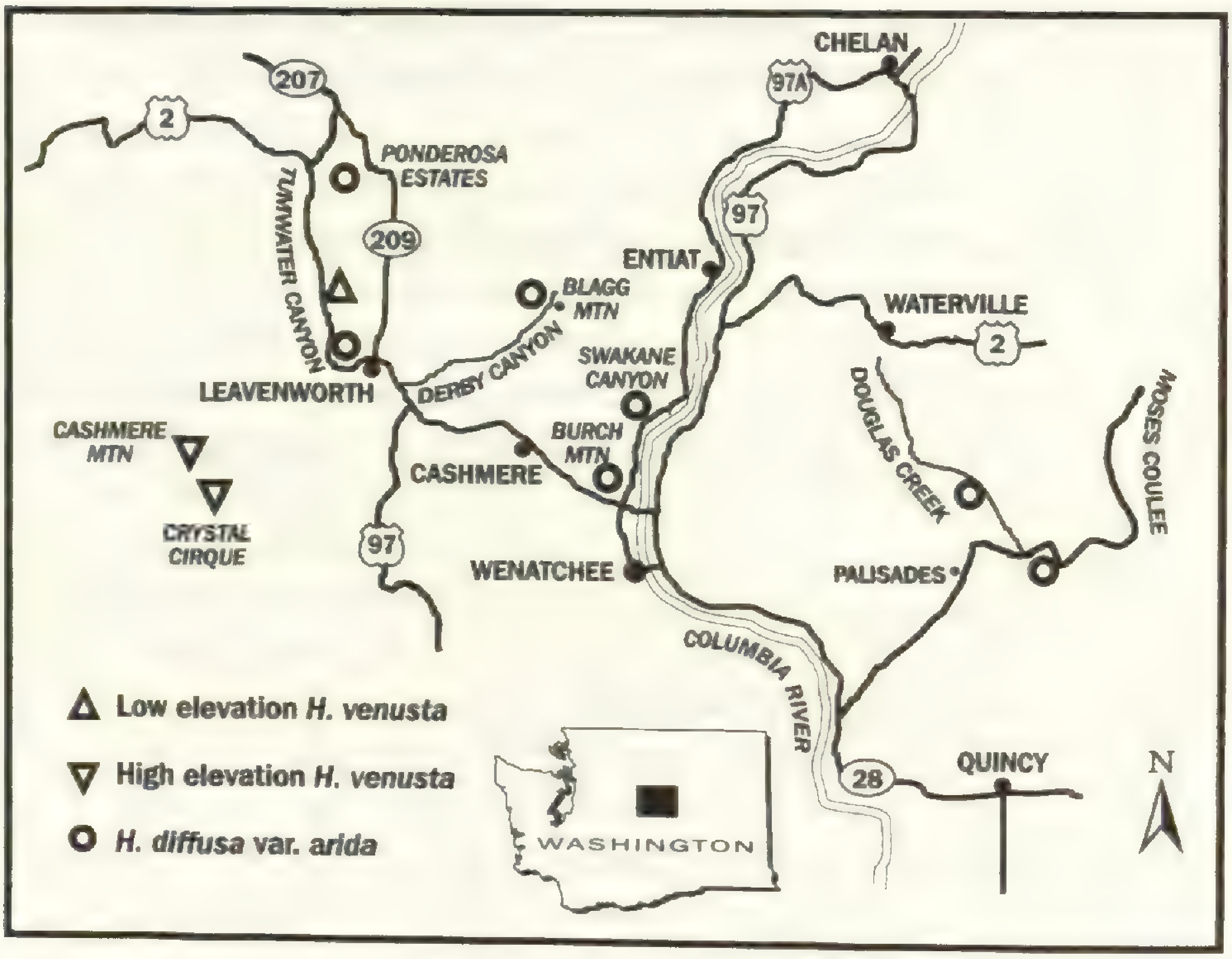
CHELAN
97A
207
2
PONDEROSA ESTATES
TUMWATER CANYON
209
97
ENTIAT
BLAGG MTN
WATERVILLE
2
DERBY CANYON
SWAKANE CANYON
LEAVENWORTH
DOUGLAS CREEK
MOSES COULEE
CASHMERE MTN
BURCH MTN
CASHMERE
CRYSTAL CIRQUE
97
WENATCHEE
PALISADES
COLUMBIA RIVER
△ Low elevation H. venusta
▽ High elevation H. venusta
○ H. diffusa var. arida
WASHINGTON
28
QUINCY
N

Figure 1. Locations of the populations of *Hackelia* examined in this study.

Leavenworth, 730 meters; Burch Mountain (BM), 4.8 km northwest of Wenatchee, 400 meters; Swakane Canyon (SC), 19.3 km northeast of Wenatchee, 1188 meters; and on the Ponderosa Estates Special Interest area (PE), 17.7 km north of Leavenworth, 670 meters. Two sites were located on Bureau of Land Management land; in Moses Coulee (MC), 24.0 km north of Quincy, 152 meters; and Douglas Creek (DC), 26.0 km north of Quincy, 140 meters.

Voucher specimens from each population of *Hackelia diffusa* var. *arida* (TW: *Malmquist 01, 02*; DE: *Malmquist 05, 06, 07*; BM: *Harrod 411*; SC: *Harrod 413*; PE: *Malmquist 08*; MC: *Malmquist 03, 04*; DC: *Harrod 349*) and from each of the Crystal Creek (*Carr et al. 3364*), Cashmere Mountain (*Kuhlmann 01*; *Benson 01*) and Tumwater Canyon (*Harrod 293*) populations of the putative *H. venusta* are deposited in the Leavenworth Ranger District Herbarium in Leavenworth. Voucher specimens from all three populations of the putative *H. venusta* (*sensu lato*) are deposited in WTU (TC: *Harrod 410*; CC: *Carr et al. 3364*; CM: *Benson 02*).

**Morphological characters.** Characters selected generally follow those used by Gentry and Carr (1976). Nineteen morphological characters from three categories were scored for statistical analysis (vegetative, floral, and fruit) and an additional 11 qualitative characters were recorded (Table 1). At each site, 25 plants were chosen randomly, numbered, and tagged. The Cashmere Mountain site, however, supports a small population and only 14 plants were selected. From each plant, one radial (basal) leaf and two cauline leaves, one from the lower one-third and one from the upper one-third of the stem, were chosen randomly for measurement. Three flowers and three fruits were chosen randomly and measured on each plant.

**Statistical analyses.** Both principal components and discriminant analyses were performed on the quantitative morphological data (SYSTAT 1997, SPSS Inc., Chicago, IL). Principal components analysis (PCA) was used to show natural groupings among each sampling unit or operational taxonomic unit (population). PCA is a method of partitioning a resemblance matrix into a set of perpendicular components (Ludwig and Reynolds 1988). Each component or axis has a corresponding eigenvalue which is the variance accounted for by that axis. The eigenvalues of the matrix are separated in descending order of magnitude so that each PCA component represents successively lesser amounts of variation (Ludwig and Reynolds 1988). The first component is the linear combination of variables accounting for more variance in the data than any other possible combination. The second component is the linear combination of the remaining variance after the first component is accounted for, the third component is the best linear combination after the first and second components have been accounted for, and so on. The data for the PCA involved the entire data set of a 238 × 19 character matrix (Table 1).

Discriminant analysis was used to establish the nonarbitrariness of group assignments. This analysis places each case within the group (population) with which it shares discriminating characters (Anderson and Taylor 1983). Unlike PCA, discriminant analysis is biased in that it positions cases within the ordination based on discriminating characters to achieve maximum separation of previously defined groups. The case distributions were plotted by two discriminant functions that separated the assigned groups to

Table 1. Morphological characters used in the taximetric analysis of *Hackelia venusta* and *H. diffusa* var. *arida*. All measurements in mm unless otherwise noted.

| Vegetative | Floral | Fruit |
|---|---|---|
| Plant height (dm) | Pedicel length | Nutlet shape (descriptive) |
| Radial leaf length | Calyx length | Nutlet surface (descriptive) |
| Radial leaf width | Calyx shape (descriptive) | Nutlet length |
| Radial leaf petiole length | Limb width | Number of intramarginal prickles |
| Radial leaf shape (descriptive) | Corolla color (descriptive) | Flange width |
| Radial leaf surface (descriptive) | Anther length | Distinct prickle length |
| Lower cauline leaf length | Fornice color (descriptive) | Fraction connate |
| Lower cauline leaf width | Fornice appendage height | |
| Lower cauline leaf shape (descriptive) | Fornice protuberance length | |
| Lower cauline leaf surface (descriptive) | | |
| Upper cauline leaf length | | |
| Upper cauline leaf width | | |
| Upper cauline leaf shape (descriptive) | | |
| Upper cauline leaf surface (descriptive) | | |

Table 2. Means and standard deviation (in parentheses) of characters used in the present study. Measurements are given in mm, except height which is in dm. [1]Abbreviations of the quantitative characters listed in Table 1.

| Character[1] | Blue-flowered *Hackelia venusta* n = 2 | White-flowered *Hackelia venusta* n = 1 | *Hackelia diffusa* var. *arida* n = 7 |
|---|---|---|---|
| Floral | | | |
| Ped | 3.7 (1.42) | 6.3 (1.88) | 4.4 (1.84) |
| Clx | 3.0 (0.43) | 3.8 (0.54) | 2.4 (0.50) |
| LimWid | 4.2 (0.72) | 7.4 (1.84) | 4.3 (0.98) |
| Anth | 0.9 (0.13) | 1.0 (0.15) | 1.0 (0.52) |
| For/Ap | 1.0 (0.14) | 1.3 (0.20) | 0.6 (0.20) |
| For/Pr | 0.8 (0.19) | 1.5 (0.31) | 0.7 (0.32) |
| Fruit | | | |
| NutL | 5.6 (0.85) | 6.4 (0.88) | 6.2 (1.14) |
| #InPr | 10.2 (2.86) | 11.4 (2.92) | 10.1 (3.93) |
| FlW | 1.8 (0.34) | 1.9 (0.38) | 1.5 (0.52) |
| DPL | 1.2 (0.25) | 1.1 (0.76) | 1.0 (0.53) |
| FrCon | 0.4 (0.11) | 0.5 (0.08) | 0.3 (0.12) |
| Vegetative | | | |
| Height (dm) | 1.4 (0.35) | 2.7 (6.74) | 5.1 (1.40) |
| RL:L | 56.9 (16.36) | 48.9 (11.6) | 98.6 (41.0) |
| RL:W | 14.4 (4.60) | 11.3 (4.08) | 8.8 (4.00) |
| RL:Pet | 21.9 (9.50) | 32.2 (10.4) | 63.3 (26.4) |
| CLL:L | 28.8 (6.64) | 37.3 (11.0) | 83.2 (23.3) |
| CLL:W | 9.2 (2.85) | 7.4 (2.00) | 4.5 (1.62) |
| CLU:L | 15.0 (5.67) | 20.1 (6.50) | 31.5 (13.3) |
| CLU:W | 6.5 (2.26) | 6.6 (2.40) | 3.7 (1.60) |

the greatest ability. Again, the data for this analysis involved the same 238 × 19 character matrix used in the PCA.

Qualitative characters were not subjected to statistical analyses, but are used for further discussion and description.

## RESULTS

The means and standard deviations for the quantitative characters are presented in Table 2 for each putative taxon. The Crystal Creek and Cashmere Mountain populations, which were blue-flowered, consistently had smaller floral measurements than the white-flowered *Hackelia venusta* of Tumwater Canyon. However, there were no consistent differences between these populations and the *H. diffusa* var. *arida* populations; there is considerable variability in floral size among populations of this latter, complex taxon. Fruit characteristics tended to be similar among all populations. The Tumwater Canyon *H. venusta* were taller in stature than the Crystal Creek and Cashmere Mountain populations, but similar to all populations of *H. diffusa* var. *arida* that were analyzed. Leaf characteristics were variable, with the Tumwater Canyon *H. venusta* having the shortest radial leaves but intermediate in leaf length for the upper and lower cauline leaves. The Crystal Creek and Cashmere Mountain populations had the widest radial and lower cauline leaves.

Radial leaf and nutlet measurements were missing from a number of cases at the conclusion of the study. These characters were dropped from both the principal components and discriminant analyses since the program would ignore those cases with missing data.

**Principal components analysis.** Each plant (case) was assigned a symbol representing its membership in the populations (OTUs) sampled. Natural groups were developed among the 238 cases by plotting the principal component scores. Of the 11 components that accounted for all the variance, the first three accounted for 68.0% (38.5%, 18.3%, and 11.2%, respectively). The groups (populations) are arranged in the ordination shown in Figure 2 based on the first two principal components. An isolated group was formed by 22 cases from the Tumwater Canyon population of *Hackelia venusta.* Two of the remaining cases were marginally associated with the *H. diffusa* var. *arida* complex and the third tended to be marginally associated with cases belonging to the Cashmere Mountain and Crystal Creek populations.

The Cashmere Mountain and Crystal Creek populations also formed a distinct group (Figure 2) although there appeared to be some overlap with cases from the Ponderosa Estates and Moses Coulee populations of *Hackelia diffusa* var. *arida.* One case from the Cashmere Mountain population was associated with Swakane Canyon, Birch Mountain, and Tumwater Canyon populations of *H. diffusa* var. *arida.*

Finally, there was considerable overlap in the *Hackelia diffusa* var. *arida* cases with no distinct groups (Figure 2). However, there is some separation based on populations; the Swakane Canyon, for example, is separated from Ponderosa Estates and Derby Canyon populations.

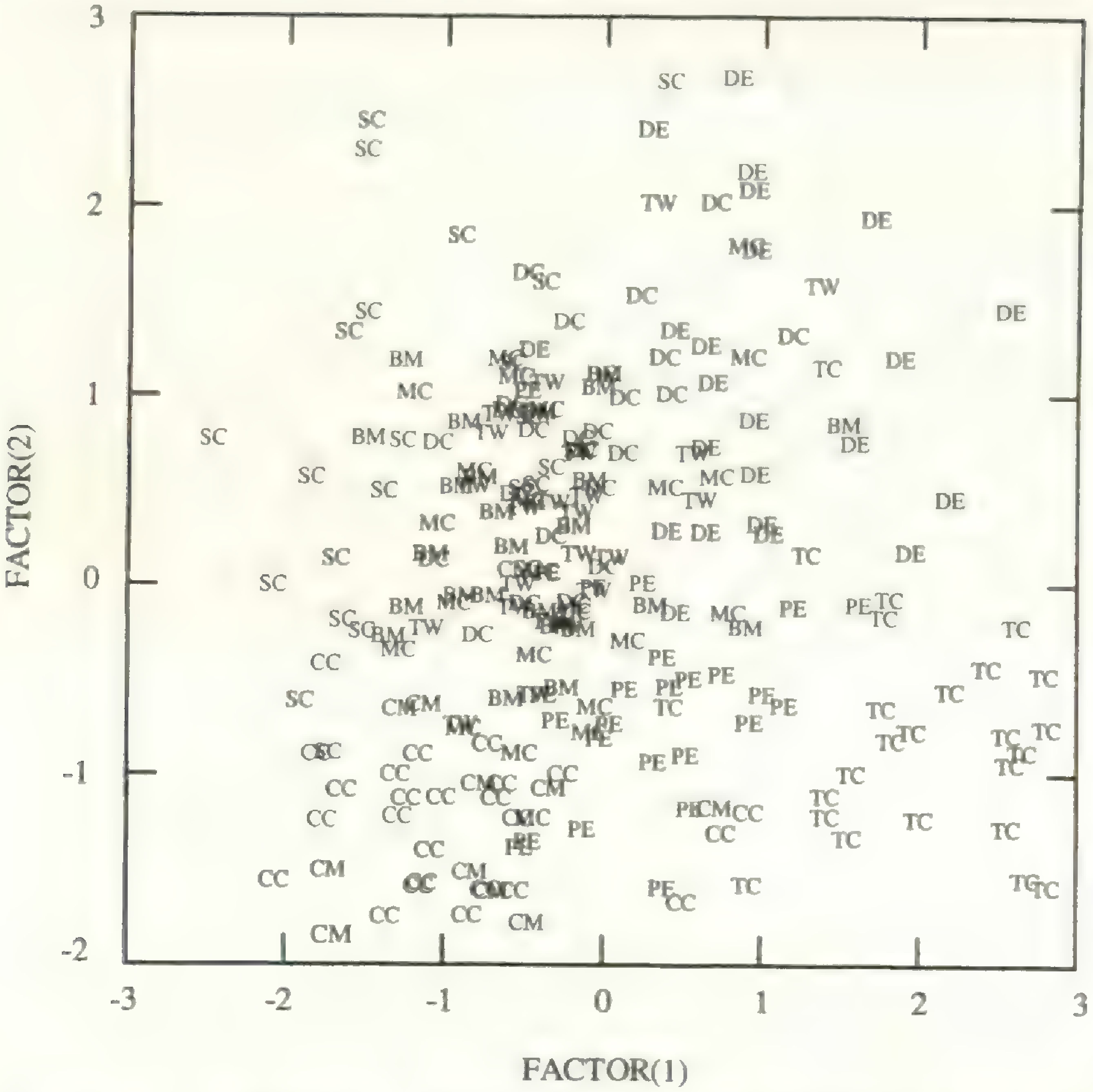

Figure 2. Ordination of populations of *Hackelia* examined in this study based on scores of principal components 1 and 2. The first two components accounted for 56.8% of the total variance (38.5% and 18.3%, respectively). *H. diffusa* var. *arida:* BM = Burch Mountain, TW = Tumwater Canyon; SC = Swakane Canyon, PE = Ponderosa Estates, MC = Moses Coulee, DE = Derby Canyon, DC = Douglas Creek; *H. venusta* (white-flowered form): TC = Tumwater Canyon; *H. venusta* (blue-flowered form): CM = Cashmere Mountain, CC = Crystal Creek.

**Discriminant analysis.** Table 3 gives the variables used and their relative usefulness in discrimination. The characters that contributed most, in order of importance, were height, fornice appendage height, fornice protuberance length, and limb width. Figure 3 shows the population centroids plotted on the basis of two (out of 9) of the most discriminating functions. Functions 1 and 2 accounted for 85.2% of the ability to distinguish among groups (72.9% and 12.3%, respectively). The total predictability

Table 3. Variables used in discrimination analysis #1 and their usefulness in discrimination among populations.

| | Function coefficients (±) | | |
|---|---|---|---|
| Variable | Function 1 | Function 2 | F (to remove) |
| Pedicel length | 0.019 | 0.158 | 5.42 |
| Calyx length | 0.271 | 0.189 | 2.78 |
| Limb width | 0.081 | 0.480 | 9.37 |
| Anther length | 0.016 | 0.013 | 1.99 |
| Fornice appendage height | 0.604 | 0.304 | 34.23 |
| Fornice protuberance length | 0.259 | 0.654 | 18.45 |
| Plant height | 0.659 | 0.072 | 48.86 |
| Upper cauline leaf length | 0.278 | 0.264 | 6.52 |
| Upper cauline leaf width | 0.153 | 0.410 | 5.71 |
| Lower cauline leaf length | 0.163 | 0.197 | 5.64 |
| Lower cauline leaf width | 0.386 | 0.228 | 3.72 |

that a case from a certain population is correctly classified to that population was 81.0%. Predictability for the Cashmere Mountain and Crystal Creek populations was 82% and 76%, respectively, with individuals not showing affinity to each population grouping with the other. Only two individuals from the Cashmere Mountain population showed affinity to another population (Tumwater Canyon, white-flowered *Hackelia venusta*). Ninety-two percent of cases were correctly classified in the Tumwater Canyon population. Predictability for the *H. diffusa* var. *arida* populations varied from 71% to 96% with deviant individuals grouping with other *H. diffusa* var. *arida* populations. The PCA showed some separation of the Swakane Canyon, Derby Canyon, and Ponderosa Estates populations, which is corroborated to some degree by the discriminate analysis (Figure 3). Predictability for the Swakane, Derby Canyon, and Ponderosa Estates populations was 96%, 83%, and 96%, respectively.

## DISCUSSION

Data collected as part of this study indicate that, as currently circumscribed, *Hackelia venusta* comprises two rather discordant elements. The original Tumwater Canyon material is clearly distinct from the high elevation collections which apparently represent an undescribed taxon. We are in the process of completing

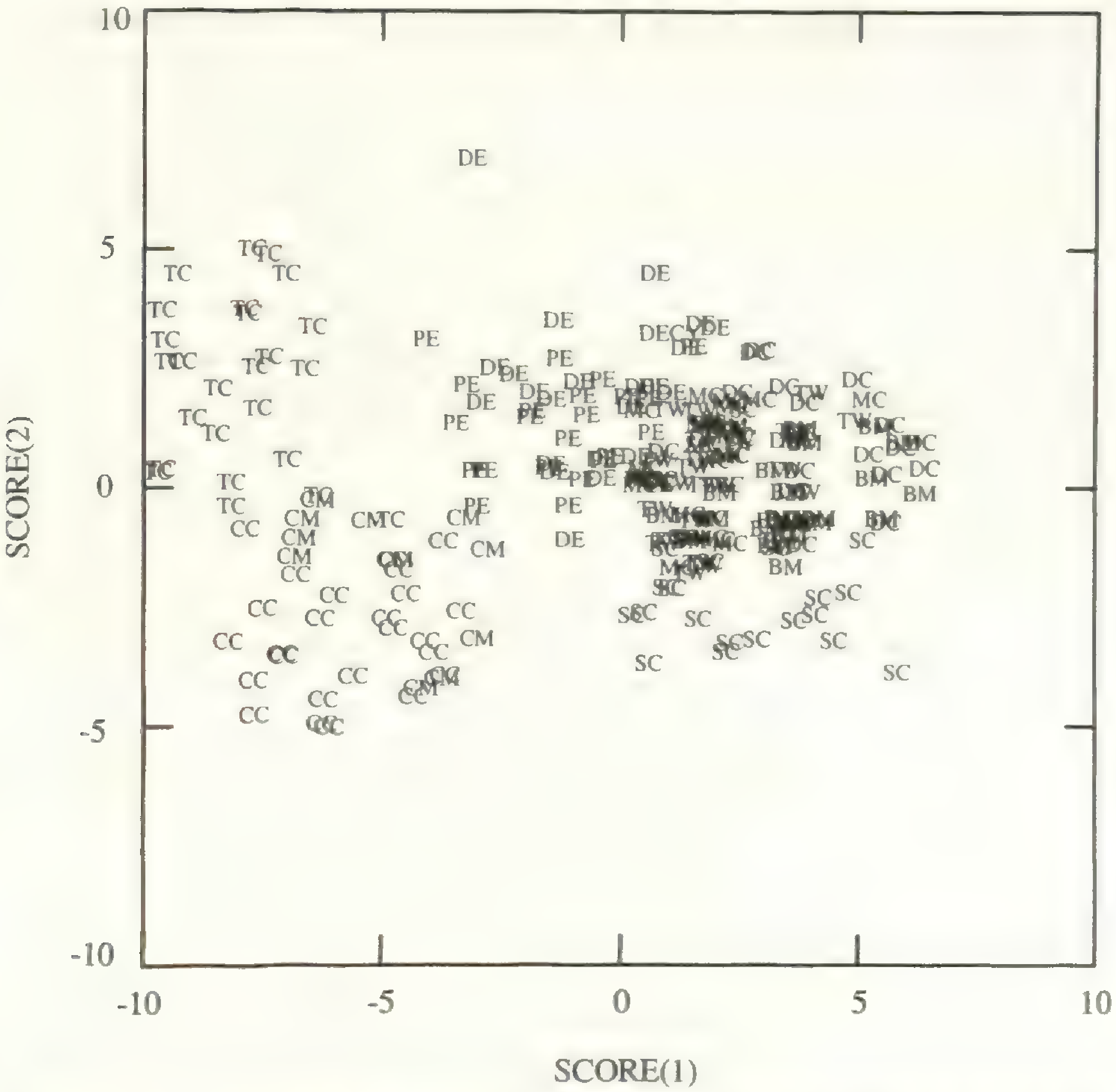

Figure 3. Ordination of populations of *Hackelia* examined in this study based on two most discriminating functions. Functions 1 and 2 accounted for 85.2% of the ability to distinguish among populations (72.9% and 12.3%, respectively). *H. diffusa* var. *arida:* BM = Burch Mountain, TW = Tumwater Canyon; SC = Swakane Canyon, PE = Ponderosa Estates, MC = Moses Coulee, DE = Derby Canyon, DC = Douglas Creek; *H. venusta* (white-flowered form): TC = Tumwater Canyon; *H. venusta* (blue-flowered form): CM = Cashmere Mountain, CC = Crystal Creek.

further studies on these and additional populations. The most obvious morphological distinction between the high elevation and Tumwater Canyon populations is flower color. The high elevation plants are always blue, while the Tumwater Canyon plants are largely white, sometimes with a faint blue tint. This study demonstrates that there are additional morphological distinctions, such as plant height, fornice appendage height, fornice protuberance length, and limb width. The high elevation and Tumwater Canyon populations also occupy markedly different environments, but both occupy similar substrate, scree derived from granodiorite and tonalite (Tabor et al. 1987). Additional factors considered include the absence of intermediate forms between the high and low elevation taxa and plants remain true to form and color when grown in a greenhouse (Harrod unpubl. data).

The results of our study do not suggest allopatric introgression between *Hackelia venusta* in Tumwater Canyon and *H. diffusa* var. *arida* as had been previously suggested by Gentry and Carr (1976). Some populations of *H. diffusa* var. *arida* do have larger flowers, but do not approach the size of the Tumwater Canyon *H. venusta* individuals. Other characters are also dissimilar. However, allopatric introgression between *H. venusta* and *H. diffusa* var. *arida* as posed by Carr (1974) and Gentry and Carr (1976) can not be ruled out by our study since we found considerable variability in floral measurements among *H. diffusa* var. *arida* populations. Three populations (Swakane Canyon, Ponderosa Estates, and Derby Canyon) were separated from each other, but not from other populations of *H. diffusa* var. *arida.* The positions of Ponderosa Estates and Derby Canyon in the PCA and discriminant ordinations were closer to *H. venusta* than any other populations including Swakane Canyon (based largely on floral characteristics). However, it is unclear from our data whether or not gradation in floral characters within populations of *H. diffusa* var. *arida* are the result of allopatric introgression or simply site differences. More information is needed to discover this possible relationship.

**Conservation concerns.** The Tumwater Canyon *Hackelia venusta* consists of one small population with ca. 150 individuals located near a major state highway. The population in the early 1970s was estimated to occupy a few hundred acres (Carr 1974; Gentry and Carr 1976), but has dramatically decreased due to highway maintenance and habitat loss associated with fire exclusion and subsequent increase in woody vegetation, shading, and stabilization of scree slopes. This population could be lost due to random environmental events and, therefore, is severely threatened. In addition, the high elevation populations are also quite restricted and may be subject to loss from stochastic events. All three populations would benefit from well-developed conservation strategies and subsequent management.

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# *MYRIOPHYLLUM MATTOGROSSENSE* (HALORAGACEAE), A RARE LOWLAND WATERMILFOIL NEW TO BOLIVIA

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ABSTRACT. *Myriophyllum mattogrossense* is reported as new to Bolivia. This rare Watermilfoil of the Amazon Basin was previously known only from the original area of discovery in Brazil, one locality in the lowlands of Peru, and one in Ecuador. Notes on morphology, including a terrestrial growth form, and habitat are given, and a key is provided to differentiate the South American taxa of *Myriophyllum.*

Key Words: *Myriophyllum*, Haloragaceae, Watermilfoil, Bolivia

Since 1994 we have been conducting a broad biodiversity survey of aquatic and wetland plants in Bolivia. While carrying out this fieldwork we encountered two small populations of *Myriophyllum* growing in streams ca. 20 km apart in the Amazon Basin region of Bolivia, known as the Chapare. The plants were found growing in swiftly flowing water of small rapids, rooted among rocks and gravel. These plants were conspicuously different from *M. quitense* Kunth (= *M. elatinoides* Gaud.), the common and widely distributed species in Bolivia. Although *M. quitense* is a common element of high elevation lakes, and is often so abundant that cattle are driven into the water to feed on it during the dry season (Dejoyx and Iltis 1991; Ritter and Crow 1998), we had not found any other populations below 2500 m and were surprised to encounter a *Myriophyllum* in the lowlands. Another species of *Myriophyllum, M. aquaticum* (Vell.) Verdc. (= *M. brasiliensis* Camb.), is a widespread aquatic weed of tropical and warm temperate regions, including northern Argentina, Paraguay, and southern Brazil (Orchard, 1981). However in Bolivia, this species is known only from a newly discovered site in the Interandean Valley Region (Ritter and Crow, in press), and it was obvious that our material was distinct from *M. aquaticum.*

We were ultimately able to determine the identity of the plant in the Chapare as *Myriophyllum mattogrossense* Hoehne, the first record known for Bolivia. Until recently, this rare species had been known only from two locations, one near Cuyabá, Mato

Grosso, Brazil, upon which F. C. Hoehne (1915) based the description for his new species, and one in the foothills on the eastern side of the Andes at Tocache Nuevo, Peru (Kahn et al. 1993; Orchard 1981). More recently, *M. mattogossense* was collected from a third location, near Coca, Ecuador (Orchard and Kasselmann 1992). Orchard (1981) noted that the species might well be found eventually in a much wider area of the lower foothills on the eastern side of the Andes of Peru, Brazil, and perhaps even Bolivia, and attributed the lack of known sites to the submerged habit and inconspicuous flowers.

Moreover, it is our experience that aquatic plants, in general, are greatly undercollected in the Neotropics. Many aquatic plants which are rather common are poorly represented in herbaria. Additional populations of *Myriophyllum mattogrossense* surely exist, but are not likely to be encountered unless the fieldwork is specifically focused on aquatic plants. This was certainly the case when Christel Kasselmann, a specialist of aquatic plants for aquarium culture, collected the first record for Ecuador (Orchard and Kasselmann 1992). We stumbled onto the first Bolivian population while searching for members of the Podostemaceae, an aquatic family restricted to rapids and swift flowing waters in areas with a seasonal fluctuation of water levels. Thus, *M. mattogrossense* is now known from its type locality in Mato Grosso, Brazil, and in the Amazon Basin near the base of the Andes in Ecuador, Peru, and Bolivia (Figure 1).

The Chapare region, where the Bolivian populations were encountered, borders the eastern slope of the Andes and is notable for having the highest amount of rainfall in Bolivia, with parts of the region receiving more than 5000 mm of precipitation per year (Ribera et al. 1994). The larger rivers and tributaries of the area experience a high level of disturbance during the rainy season. River courses in the Chapare are extremely transitory, with riverbeds receiving large depositions of gravel and sand, and with new channels frequently being formed while former stretches are transformed into *curiches* (oxbows). Streams and other tributaries can also experience significant disturbance as well. Generally speaking, the streams in the area are characterized by a lack of rooted vegetation and haptophytes (Crow and Ritter, pers. obs.). In the case of *Myriophyllum mattogrossense,* it appears that a combination of fairly specific habitat requirements—clear, fast-moving water and a substrate composed of gravel and cobbles—

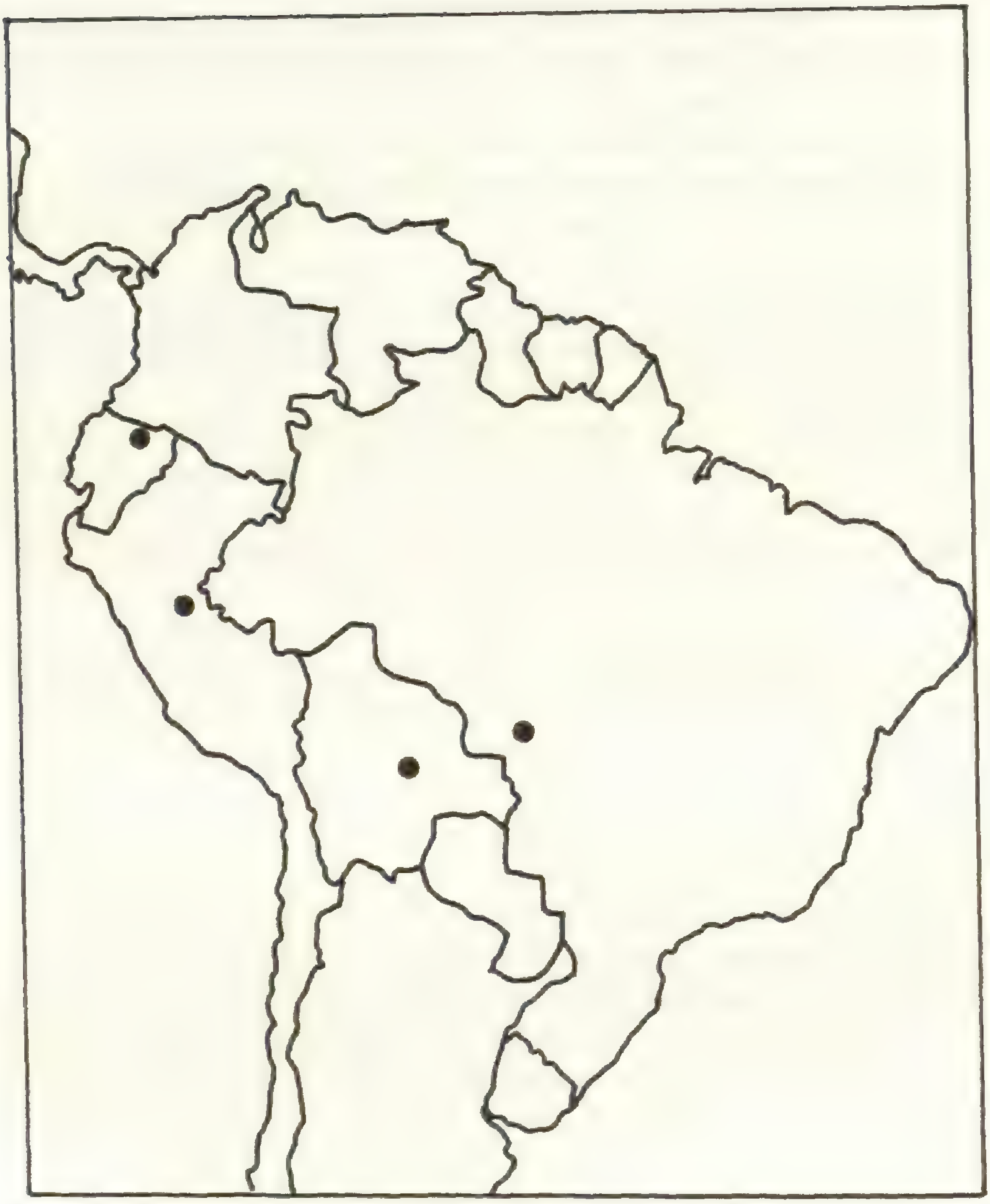


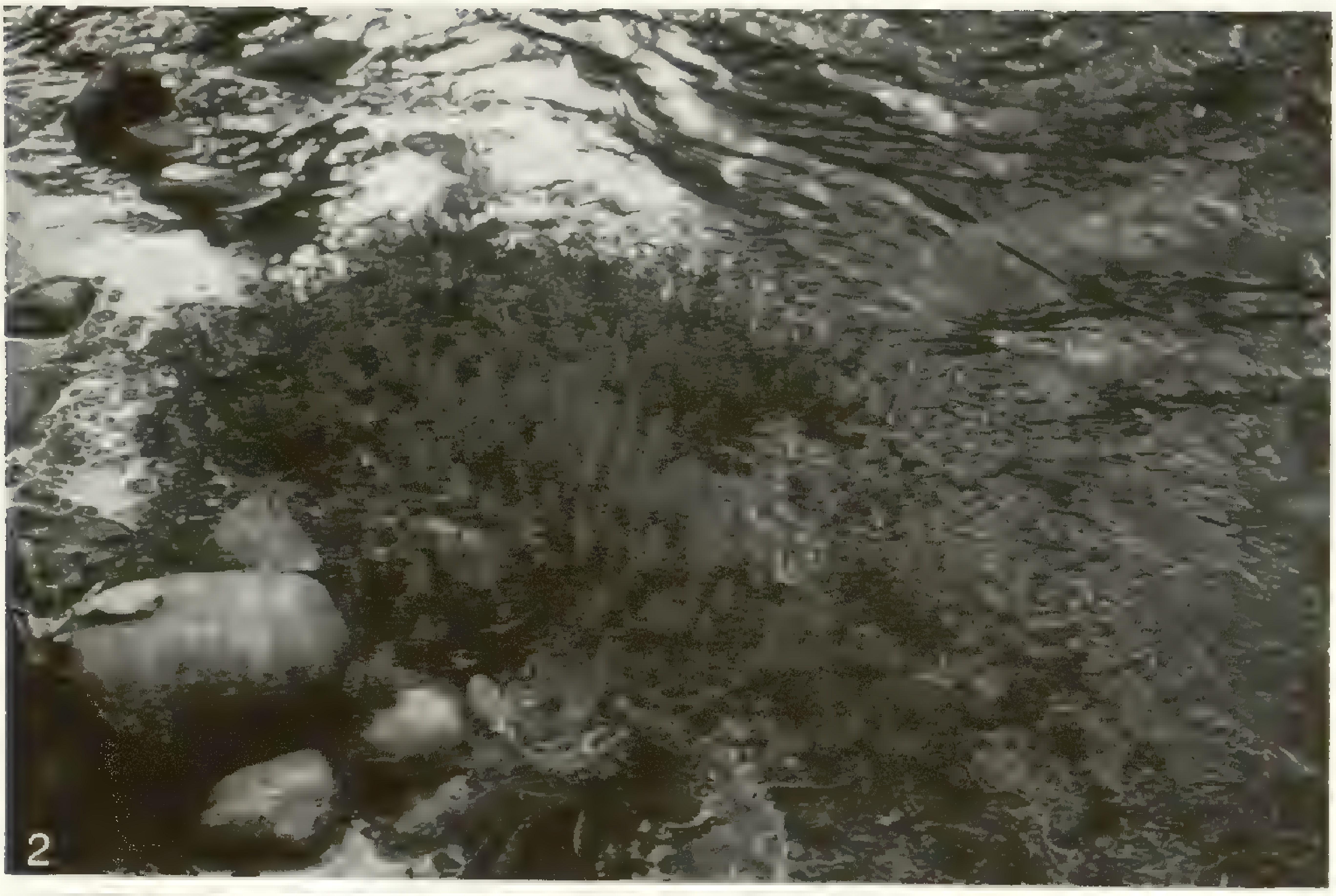
Figure 1. Documented distribution of *Myriophyllum mattogrossense*.

coupled with the transitory nature of aquatic habitats due to severe disturbances, serves to limit the number of populations of this species.

Previously, this species was believed to be strictly submersed. Orchard (1981) stated that the species is unusual in that its flowers and fruits are unusually small, and that the plant was reported to grow completely submersed, resulting in underwater opening and pollination of the flowers. While we observed the submersed plants to be fertile, as did Hoehne (1915), we also observed the existence of a terrestrial growth form for *Myriophyllum mattogrossense,* likewise in fertile condition. The terrestrial growth form was initiated as the water level dropped and marginal plants became stranded (Figure 2). The submersed leaves dried up and new upright branches sprouted from the prostrate stem. When seen in this condition, the species had an almost moss-like, or *Hippurus*-like appearance (Figure 2). Although this was observed in both of the Bolivian populations, there was no mention of a terrestrial growth form on the labels of the Peruvian specimens examined. However, Kasselmann (Orchard and Kasselmann 1992) observed emergent plants growing on mud along the riverbank, which fit the description of the terrestrial growth form we observed.

In the Bolivian material the leaves of submersed plants have segments that, while filiform, are very thin, distinctly flattened, with a conspicuous midvein, and which are wider than typical for *Myriophyllum quitense.* The Peruvian material examined exhibited the same morphology. We were able to examine only one herbarium specimen of the Ecuadorian material, and while the submersed leaves were flattened, the segments were much more filiform than those of either the Bolivian or Peruvian material. However, they did closely resemble those depicted in the illustration accompanying Hoehne's (1915) original description, now serving as the lectotype (Orchard 1981). Previously, we had noted that the markedly capillary leaf segments in the Brazilian population were altogether distinct from those of the other populations. We were able to reconcile this variation by attributing it to habitat differences (*lacus temporarius* in Brazil). Arber (1920) noted that water plants respond to certain physical stimuli and that in *Myriophyllum,* in particular, one can observe marked differences in the morphology of the same species growing in different current regimes. In still water, plants may have leaf segments that are delicate and nearly hair-like, while the stresses of current on the leaves of plants growing in strongly flowing water require that leaves tend toward increased mass and thickness (Arber 1920; Gerber and Les 1994).

In contrast to the submersed plants, the leaves of the terrestrial form have divisions that, while still somewhat flat, are pectinate (with fewer divisions), thicker, and distinctly succulent (Figure



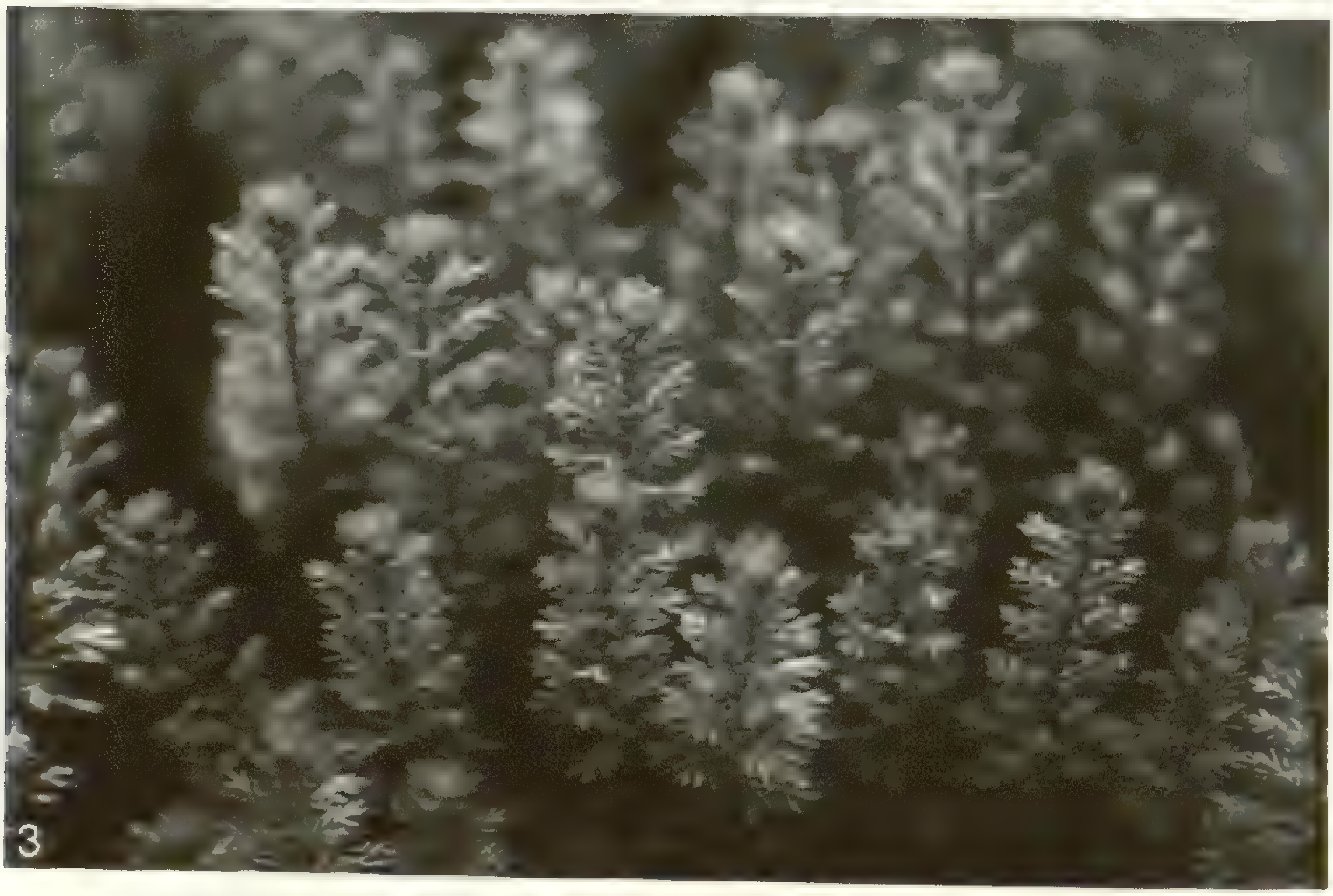


Figure 2. Habit of terrestrial growth form of *Myriophyllum mattogrossense* at edge of stream.

Figure 3. Close-up view of terrestrial growth form of *Myriophyllum mattogrossense* showing somewhat flattened, thicker, succulent, pectinate leaves.

3). The flowers and fruits are axillary on both terrestrial and submersed plants.

### DESCRIPTION OF BOLIVIAN MATERIAL

Plants perennial, herbaceous aquatics, with submerged and terrestrial growth forms (Figure 4). Stems and leaves with small sessile glands; glands moderately dense on young growth, becoming sparse on older growth. Submersed growth form: stems flexuous, ascending in quiet water, somewhat horizontal in flowing water; leaves verticillate, in whorls of 3–4, pinnately divided, ca. (18–)20–22(–25) mm long, with 7–8 pairs of lateral segments (mostly alternate), segments flattened, 0.4–0.5 mm wide, each with a distinct midvein; hydathodes filiform, tiny, present at base of petioles and each leaf segment on young growth. Terrestrial growth form: stems of submersed plants rooting on stream margins or gravel bars, submersed leaves withering away; upright stems arising from axillary buds, not flexuous, sturdy, erect; leaves verticillate, pectinate, mostly 10–11 mm long, becoming shorter toward stem tip (4–5 mm long), mostly with 3 pairs of lateral segments (alternate), segments somewhat flattened, thickish, slightly succulent, each with a distinct midvein (especially on herbarium material) each segment with an apical secretory gland; hydathodes filiform, tiny, present at base of petioles and each leaf segment on young growth. Flowers (both growth forms) axillary, 1–4 per whorl, bisexual, appearing sessile (pedicel short, 0.25–0.4 mm long), subtended by a pair of bracteoles (apparently early caducous), frequently with filiform hydathodes on each. Perianth 4-merous, opposite the ovary lobes, alternate with stamens. Stamens 4, subsessile, anthers ovoid, slightly apiculate at tip, stamens developing before stigmas, not long persisting. Ovary inferior, 4-lobed, stigmas 4, conical; tiny hydathodes present at summit of ovary. Fruits globose, 4-lobed, 7–9 mm long, 7–9 mm wide; mericarps with a few weak tubercles on outer surface.

Flowering in this species did not appear to be seasonal. Based on all specimens examined, flowering material has been observed on specimens collected in February, March, April, May, June, and November.

Orchard and Kasselmann (1992) noted a number of features evident in the Ecuadorian populations which had not previously been observed in *Myriophyllum mattogrossense,* thus expanding

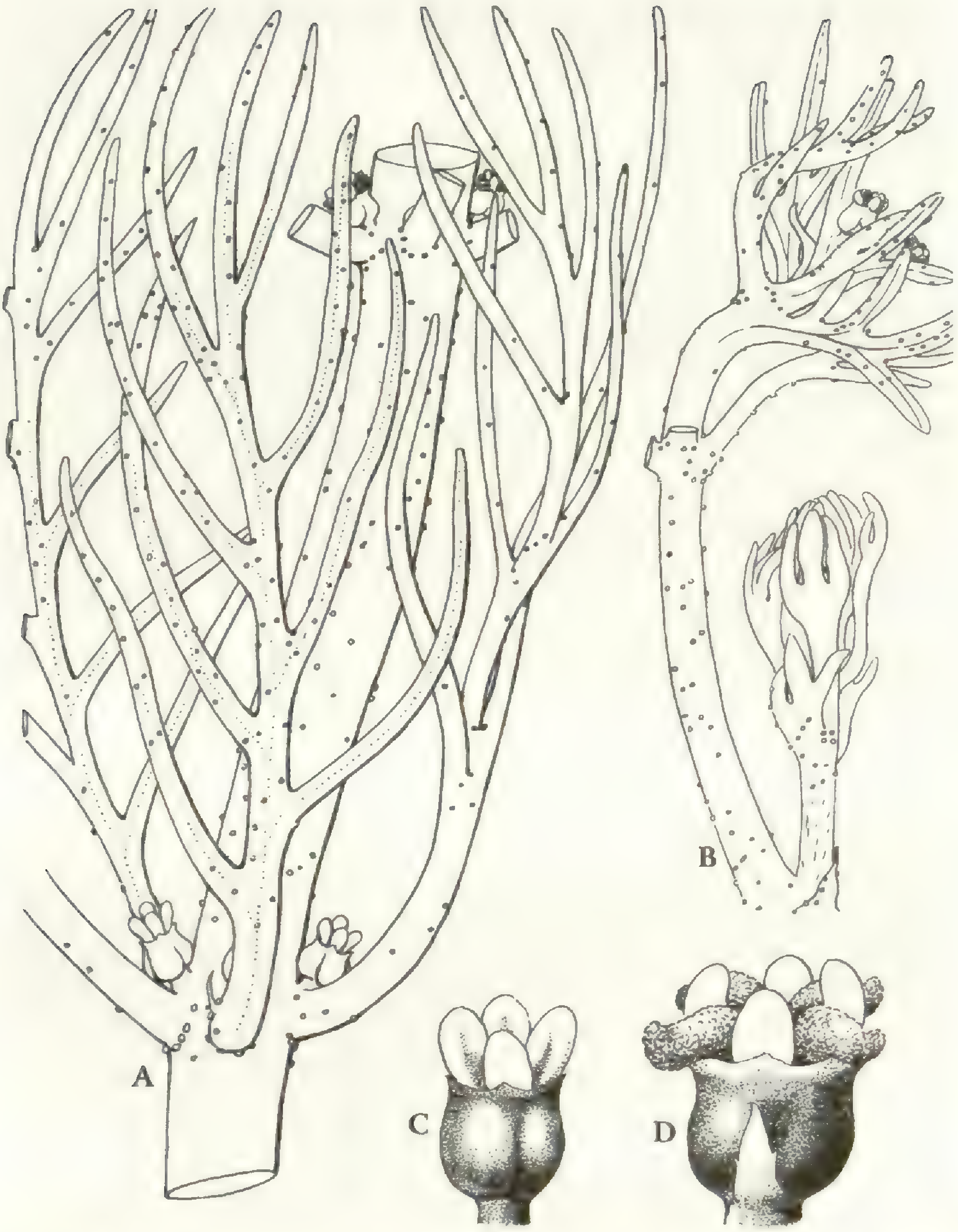


Figure 4. *Myriophyllum mattogrossense* drawn from submersed growth form specimens. (A) Section of stem showing axillary flowers, glandular emergences (appearing as dots) scattered on leaves and stems, and hydathodes present at leaf bases. (B) Section of young shoot. (C) Young flower with only stamens evident. (D) Mature flower with stigmas alternating with stamens, and with subtending bracteole present.

the description for the species. These features were, in particular, the presence of filiform "hydathodes," the *trichomas collectores* of Hoehne (1915), at the bases of the petioles and at the base of each leaf segment on young growth; the presence of numerous, scattered, globular sessile glands on the surface of the young stems and leaves; and flowers with a complete absence of a perianth. The Bolivian material is consistent with all of these features with exception to that of the perianth. In the Bolivian specimens the flowers do possess a single, 4-merous perianth whorl of small triangular appendages, arranged alternate the styles and opposite the 4 stamens, the stamens developing first and not persisting. A further character we noted was the presence of a pair of bracteoles subtending the flowers (Figure 4), which apparently are caducous, as they were noted only with earlier stages of flowers. *Myriophyllum mattogrossense* had previously been described as lacking bracteoles (Orchard 1981; Orchard and Kasselmann 1992); a lack of bracteoles is unusual in the family (Orchard and Kasselmann 1992).

The presence of sessile glands is unusual in the genus (Orchard and Kasselmann 1992), thus the feature can serve as a good diagnostic character for *Myriophyllum mattogrossense*. Since glands had not been noted on the Peruvian material (Orchard 1981), we re-examined the Peruvian herbarium specimens; globular sessile glands are, indeed, present.

Recently, some puzzling reports of *Myriophyllum mattogrossense* in the Gran Pantanal of Mato Grosso, Brazil, have appeared in the literature. Prado et al. (1994) noted that *M. mattogrossense* forms "luxuriant beds" during the high water stages in the Pantanal. This species was said to "bloom intensively" during this time, and then to die off. The authors stated that *M. mattogrossense* is "easily recognized in the field by its deep red, densely clustered leaves," and further noted that the species possesses emergent flowers which descend below the water's surface following fertilization (Prado et al. 1994, p. 581). Clearly, red vegetation and emergent inflorescences are characters not known to be associated with *M. mattogrossense*. Unfortunately, the identity of their plants cannot be confirmed as no voucher specimens had been cited.

Heckman (1997) reported *Myriophyllum mattogrossense* as filling the niche of submersed plants in the tropical wet-and-dry climatic zone in South America. In a subsequent book on the

Brazilian Pantanal, he described "luxuriant submerged beds" of *M. mattogrossense* that form in the northern Pantanal during the high water stage, and included a color photograph of the presumed *M. mattogrossense* (Heckman 1998). Having examined this photograph, we have concluded that the species in question is clearly not *M. mattogrossense.*

Although Pott and Pott (1997) included *Myriophyllum mattogrossense* in their comprehensive checklist of aquatic plants of the Brazilian Pantanal, they noted that they have never observed this species in the Pantanal, and were aware of its presence only through the original type collections of Hoehne (Vali Pott, pers. com., 1998). Furthermore, Guarim Neto's (1992) checklist of angiosperms of the Pantanal includes no species of *Myriophyllum.* In like manner, during our extensive expedition in 1998 in the Bolivian portion of the Pantanal we encountered neither *M. mattogrossense* nor any other species of *Myriophyllum.*

### SPECIMENS EXAMINED

**Bolivia.** Department of Cochabamba: Province of Carrasco, road between Comunidad Ivirgarsama and Puerto Villarroel, ca. 18.5 km south of town, 16°59′08″S lat., 64°49′20″W long., elev. ca. 200 m, rooted among rocks in fast-moving water in the Arroyo Magareños, just below where it crosses the road, 19 Mar 1995, *Ritter 1678*; 8 Jun 1995, *Ritter & Crow 2313* (aquatic form); 8 Jun 1995, *Ritter & Crow 2314* (terrestrial form; LPB, MO, NHA).

**Bolivia.** Department of Cochabamba: Province of Carrasco, Arroyo Zabala, just below where it crosses the highway to Santa Cruz, 17°06′S lat., 64°40′W long., elev. ca. 230 m, rooted among cobbles and gravel in clear, fast-moving water, 5 May 1996, *Ritter 3147* (LPB, MO, NHA).

**Brazil.** Mato Grosso, near Cuyabá. Original specimens of F. C. Hoehne apparently lost (Orchard 1981). LECTOTYPE: Tabula n. 127 ("Ns. 4.578 e 4.635. Hab. lacus temporarius ad Coxipó da Ponte, propre Cuyabá"), Comm. Linh. Telegr. Mato Grosso Amaz., Annexo 5, Bot. 6. 1915.

**Ecuador.** Río Coca, 8 Feb 1990, *Kasselmann 133* (B). According to Orchard and Kasselmann (1992) the site locality is: Río Yanaucu (lower Río Coca drainage) about 20 km north of the town of Coca (Pto. Francisco de Orellana) at the crossing of the road from Coca to Lago Agrio.

**Peru.** Department of San Martín: Province of Mariscal Cáceres, al oeste de vivero del Instituto Agropecuario de Tocache, Tocache Nuevo, elev. 400 m, 10 Nov 1969, *Schunke V. 3598* (GH, US).

**Peru.** Department of San Martín, Province of Mariscal Cáceres, Fundo Jeroglífico, del Sr. Luís Ludeña (Quebrada de Ishichimi), Tocache Nuevo, elev. 400 m, 10 Apr 1975, *Schunke V. 8281* (MO).

**Peru.** Department of San Martín: Province of Mariscal Cáceres, Quebrada Ishichimi, cerca al Fundo del Sr. Luis Ludeña, sumergida en las riachuelos, elev. ca. 400 m, 3 Nov 1980, *Schunke V. 12393* (MO).

In order to facilitate differentiation of the species of *Myriophyllum* in South America the following key is provided, including information from our expanded understanding of *M. mattogrossense* and *M. quitense* (Ritter and Crow 1998). Additionally, it is noteworthy that although *M. spicatum* L. has been listed for Peru and *M. verticillatum* L. has been listed for Chile, specimens bearing those names were based on misidentified specimens (Orchard, 1981); these two species are not known to occur in South America.

### KEY TO THE SOUTH AMERICAN SPECIES OF *MYRIOPHYLLUM*

1. Submersed leaves in whorls of (2–)3–4(–5); segments of submersed leaves very slender, distinctly flattened, ca. 0.5 mm wide, with conspicuous midvein, or filiform; emergent leaves absent on submersed form in reproductive phase (terrestrial growth form, with ascending aerial branches sprouting from prostrate stems, may be expected to occur stranded along water margin; leaves pectinate, mostly 10–11 mm long, segments mostly 3 per side); leaves and stems bearing scattered, small, globular, sessile glands (especially young material); flowers solitary, borne axillary along submersed portion of stem, (also axillary along erect stems on terrestrial form); flowers bisexual; stamens 4; mericarps with a few weak tubercles on outer surface; rare, lowlands, Ecuador, Peru, Bolivia, and Brazil ...... ................................ *M. mattogrossense*

1. Submersed leaves in whorls of (3–)4–6; segments of submersed leaves filiform to only somewhat flattened, mostly up to ca. 0.25 mm wide, midvein not conspicuous; emergent leaves present on submersed form (terrestrial form rare in *M. quitense*; ascending aerial branches sprouting from prostrate stems, leaves pectinate, mostly 7–10 mm long, segments 5–6(–8) per side); leaves and stems lacking glands; flowers in spicate inflorescences, borne in the axils of the emergent leaves only; flowers unisexual, plant monoecious or dioecious (bisexual flowers on terrestrial form in *M. quitense*); stamens 8; mericarps smooth on outer surface ........................................ (2)

   2. Submersed leaves in whorls of (3–)4(–5), ovate in outline, 1–2 cm long, with 7–9 pairs of pinnae, segments nearly

filiform, somewhat flattened; emergent leaves blue-green, tinted red or purple, in whorls of (3–)4, ovate to oblong, more or less entire, at least in upper parts, toothed to pinnatisect in lower parts; plants monoecious (flowers bisexual in terrestrial form); Andes from Venezuela to Tierra del Fuego, e. Argentina, s. Uruguay, and Falkland Islands, disjunct (introduced?) in Mexico, nw. North America, P.E.I., Canada ..... *M. quitense*

2. Submersed leaves in whorls of (4–)5–6, oblanceolate in outline, (1.7–)3.5–4 cm long, with 12–15 pairs of pinnae (lower leaves decaying rapidly); distinctly filiform, terete; emergent leaves glaucous, in whorls of (4–)5–6, narrowly oblanceolate, pectinate, with (9–)12–18 pairs of pinnae; plants dioecious (female plants only in adventive populations); s. Peru, s. Bolivia, and s. Brazil south to c. Chile, n. Argentina, and Uruguay, introduced weed northward in Mesoamerica and e. and nw. U.S. .............................. *M. aquaticum*

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# DISTRIBUTION AND DENSITY OF SUBMERGED AQUATIC VEGETATION BEDS IN A CONNECTICUT HARBOR

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ABSTRACT. Submerged aquatic vegetation (SAV), *Zostera marina* and *Ruppia maritima,* was surveyed and mapped for an inventory of inner Clinton Harbor, Clinton, Connecticut. Transects set at 30 meter intervals were established along the northern shoreline of the inner harbor, and SCUBA was utilized to count SAV short shoot densities. Surveys revealed that the majority of the inner harbor was dominated by nine areas (ca. 11 ha) of low density seagrass beds. In addition, nine areas (ca. 6.5 ha) of high density seagrass beds and ten areas (ca. 5.5 ha) of medium density seagrass beds were located. No SAV was found in the navigational channel or upon the mudflat along the northern shore of the inner harbor.

Key Words: SAV, distribution, Long Island Sound, Clinton Harbor

Submerged aquatic vegetation (SAV) of the North American Atlantic coastal waters supports highly diverse animal assemblages (Heck et al. 1989; Rozas and Odum 1987). Seagrass beds function as refugia, energy sources, and habitat for the animals inhabiting the beds (Heck et al. 1989; Sogard and Able 1991). A decline in seagrass bed production would have profound effects upon these animal assemblages and would decrease detrital export, greatly reducing energy sources for other fauna not directly inhabiting SAV beds (Thayer et al. 1984).

The reduction of SAV in the coastal United States has been well documented (Kemp et al. 1983; Orth and Moore 1983; Roblee et al. 1991; Thayer et al. 1994). Natural causes of SAV decline such as disease, storm events, salinity fluctuations, and hypoxic events coupled with anthropogenically induced eutrophication currently threaten the production of many SAV communities (Durako and Kuss 1994; Koch and Beer 1996; Montague and Ley 1993; Olesen and Sand-Jensen 1994; Zieman et al. 1994). Therefore, documenting the distribution of SAV is important in developing baseline data which can be used to monitor abundance patterns and ecological health over extended periods of time.

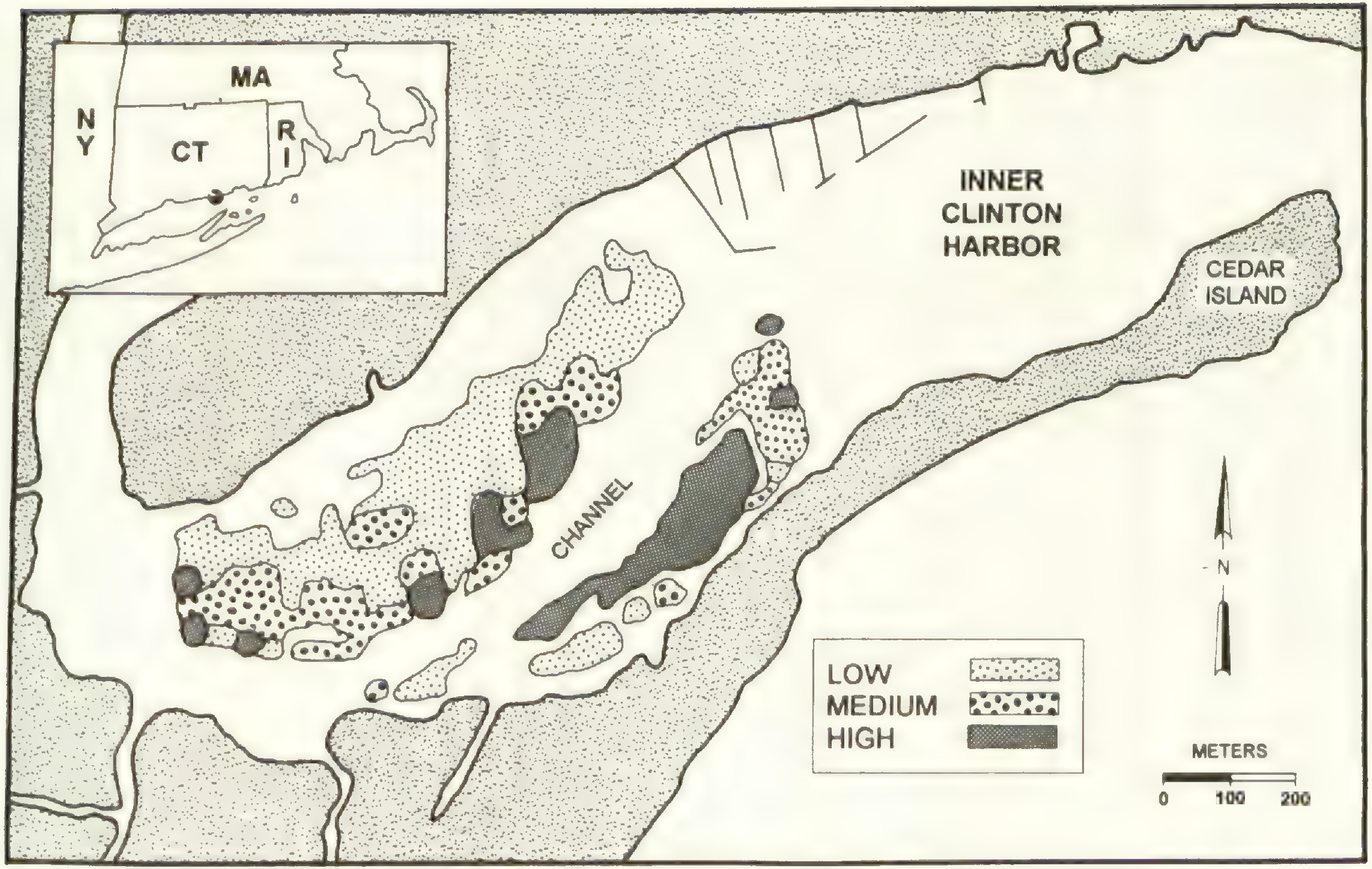
The distribution of SAV (*Zostera marina* L. and *Ruppia maritima* L.) along the Connecticut coast of Long Island Sound has been previously documented by Koch and Beer (1996). However, detailed maps of the extent of seagrass beds within individual bays and harbors are not available. Historically, SAV has been reported to occur in Long Island Sound as far west as New York State but is now limited to the easternmost third of Long Island Sound (Koch and Beer 1996). Clinton Harbor is considered the westernmost distribution point of seagrass in Long Island Sound (Koch and Beer 1996) and was selected as a study site to monitor changing SAV distribution patterns. The purpose of this study was to provide baseline information on the density and the distribution of SAV in inner Clinton Harbor (Clinton, CT).

Clinton Harbor occupies 162 ha and is located on the Connecticut shore of Long Island Sound. The harbor is a drowned river valley inundated by seawater and receives freshwater input from the Hammock, Indian, and Hammonasset Rivers. Inner Clinton Harbor is the mouth of the Hammonasset River and is formed by the presence of the Cedar Island spit (Figure 1). The tides within the harbor are semi-diurnal and display a mean tidal range of 1.5 meters. Clinton Harbor is a rural harbor with 60% of its bordering land edge being utilized as wetlands and beaches, 25% as marinas, and 15% as residential housing (Mroczka 1991).

## MATERIALS AND METHODS

SAV densities were measured in inner Clinton Harbor from August 15, 1990 through October 31, 1990. Inner Clinton Harbor was divided into 33 transects set at 30 m intervals along the shoreline. The transect positions were established with survey equipment, marked with stakes, and subsequently plotted on a hydrographic survey map.

SAV densities were obtained using SCUBA. Divers moved


MA
N Y
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ISLAND
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N
LOW
MEDIUM
HIGH
METERS
0
100
200

Figure 1. Map of inner Clinton Harbor indicating the location and density of submerged aquatic vegetation. Density categories are expressed as the mean number of short shoots per m$^2$ (Low = 0–20; Medium = 21–40; High $\geq$ 41).

along a calibrated 200 m line making observations at 15 m intervals. At each interval, SAV short shoot densities were counted in two randomly placed 0.5 $m^2$ grids. *Zostera marina* and *Ruppia maritima* short shoots were not differentiated in the counts. Counts were adjusted to $m^2$ values and the mean of the two counts was then calculated and used as a datum point for mapping. A total of 662 sampling points, each sampled once, was used in this study. SAV distribution was plotted on a survey map (Figure 1) using the density categories established from percent shoot coverage of a $m^2$ grid. The densities established were categorized as low (0–20 short shoots per $m^2$), medium (21–40 short shoots per $m^2$), and high ($\geq$41 short shoots per $m^2$). Area covered (ha) was then calculated for each density category with a Scalex Planwheel planimeter.

## RESULTS

SAV was documented in an estimated 23 ha of inner Clinton Harbor. Although *Zostera marina* and *Ruppia maritima* shoots were not differentiated in the counts, the beds were dominated by *Z. marina.* Nine areas of low density SAV beds were identified (Figure 1). The low density beds were distributed throughout the study area, but were located primarily in areas north of the navigational channel. Low density beds occupied approximately 11 ha. Nine areas of high density SAV beds, occupying approximately 6.5 ha, were located laterally along the navigational channel (Figure 1). Ten areas of medium density beds were also identified laterally along the navigational channel (Figure 1). Medium density beds accounted for approximately 5.5 ha of all SAV beds. The mudflat along the northern shore of the inner harbor was unpopulated by SAV, as was the navigational channel.

## DISCUSSION

Seagrass beds play integral roles in coastal ecology and have been suggested to be among the most productive aquatic ecosystems known (Day et al. 1989). Extensive declines in SAV along the coastal United States in the past few decades have made it necessary to document and monitor the extent of existing seagrass beds (Koch and Beer 1996; Olesen and Sand-Jensen 1994). Baseline data of SAV distribution will provide researchers and resource managers with the necessary information to begin to recognize and interpret the effects of both natural and anthropogenic impacts on the seagrasses, which will be critical for the future management of this resource.

The results of our 1990 survey have shown that inner Clinton Harbor was dominated by low density seagrass beds (Figure 1), which were located mainly in the areas north of the navigational channel. This portion of the harbor is dominated by poorly sorted mud/silt deposits (Mroczka 1991) and is typically exposed during periods of normal low tide. High turbidity significantly reduces light availability and the production of the beds throughout this area.

High and medium density SAV beds were identified in large aggregations laterally along the navigational channel (Figure 1). High flow rates of water through the navigational channel keep the surrounding sediments composed of well sorted sand grains (Mroczka 1991). High water flow also reduces the turbidity in the areas surrounding the channel making the water considerably clearer than that of the mudflats to the north. Water clarity in these areas permits the critical light level to extend to the bottom, allowing for more productive seagrass beds (Day et al. 1989; Duarte 1991).

The lack of SAV within the navigation channel is due to the depth of the channel and periodic oyster dredging. The 3 m depth of the navigational channel does not allow sunlight to penetrate to a level that is conducive to SAV growth (Duarte 1991). Periodic oyster dredging in the channel also precludes the establishment of SAV beds.

Our study provides baseline data on the general distribution of SAV in inner Clinton Harbor. Future SAV monitoring can be conducted and subsequently compared to the results of this survey in order to determine changes in the distribution patterns of the seagrass beds.

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# THE DISTRIBUTION OF THE BRYOPHYTES AND VASCULAR PLANTS WITHIN LITTLE DOLLAR LAKE PEATLAND, MACKINAC COUNTY, MICHIGAN

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ABSTRACT. Little Dollar Lake peatland, a *Sphagnum*-dominated poor fen peatland complex, has a flora consisting of 36 bryophyte and 93 vascular plant species. Random, quantitative sampling of 279 one-meter-square quadrats along 13 transects on six peatland mats was analyzed by two-way indicator species analysis (TWINSPAN). Based on interpretation of the TWINSPAN analysis, three vegetation cover types and six constituent vegetation phases were delineated. The three cover types were designated as the *Calamagrostis canadensis* cover type (lagg habitats), the *Chamaedaphne calyculata* cover type (peatland mat habitats), and the *Chamaedaphne calyculata–Triadenum fraseri* cover type (transitional habitats with evidence of terrestrialization). A fourth association, the *Potamogeton confervoides–Utricularia geminiscapa* cover type, was recognized based on qualitative field observations and consisted of the aquatic vegetation within Little Dollar Lake. Botanical evidence suggests that terrestrialization and small-scale paludification are occurring in some areas of the peatland.

Key Words: peatland, bog, fen, *Sphagnum*, bryophytes, vascular plants, terrestrialization, TWINSPAN, Michigan

Peatlands are wetlands especially characteristic of northern regions across North America and Eurasia that form in cool, temperate or maritime climates where evapotranspiration is low. Peat deposits dominate the boreal environments of Canada ($170 \times 10^6$ ha), the former Soviet Union ($150 \times 10^6$ ha), and the United States ($36.8 \times 10^6$ ha; Gorham 1990). Near the southern edge of the glacial boundary in North America, peatlands tend to be more sporadic and are usually confined to smaller areas (typically glacial scour basins or kettleholes), as opposed to the extensive mires that blanket the landscape of subarctic latitudes (Crum 1988). Along the glacial boundary, peatland basins are frequently frost pockets that serve as refugia for northern plants at the southern edge of their ranges (e.g. Andreas and Bryan 1990; Crum 1988; Damman and French 1987; Pielou 1979).

The peat of boreal regions consists of partially decomposed remains of bryophytes (especially *Sphagnum*) and vascular plants (primarily sedges and ericaceous shrubs), as well as minute amounts of inorganic matter (Crum 1988; Damman and French 1987; Moore and Bellamy 1974). Although the majority of wetlands produce peat to some extent, northern peatlands store vast quantities of peat because rates of organic deposition greatly exceed rates of decomposition (Crum 1988).

Peatlands are typically associated with acidic water chemistry. The main causes of peatland acidity are the result of a variety of biogeochemical processes and positive feedbacks (Crum 1988; Gorham 1957; van Breeman 1995) involving the presence of organic acids within the anoxic subsurface peat (Hemond 1980; Kilham 1982), the high cation exchange capabilities of *Sphagnum* taxa (Andrus 1986; Clymo 1963, 1964; Crum 1988; Kilham 1982; Spearing 1972; Vitt et al. 1975), the uptake of ions by vegetation (Kilham 1982), the overall hydrological characteristics of individual peatland systems (Kilham 1982; Vitt et al. 1975), the oxidation of reduced sulfur compounds (Clymo 1964; Gorham 1961), and, occasionally, acid precipitation (Clymo 1964; Crum 1988).

Conditions within peatlands are generally considered less than optimal for vascular plant growth and establishment (Clymo and Hayward 1982; Moore and Bellamy 1974; van Breeman 1995; Vitt et al. 1995). However, extensive bryophyte communities thrive in peatland environments of boreal landscapes (Vitt 1990). Due to their intimate contact with the aqueous chemical environment of the peatland, bryophytes are strong indicators of microhabitat conditions (Vitt and Slack 1984). Peatland vegetation distributes itself based largely on gradients of minerotrophy (e.g. alkalinity) and pH, as well as light and hydric conditions of microhabitats (e.g. Anderson and Davis 1997; Gignac and Vitt 1994; Jeglum 1971; Vitt and Chee 1990; Vitt and Slack 1975; Wheeler et al. 1983).

Peatlands exhibit strong floristic similarities across much of North America, resulting in similar species composition patterns in regions such as the Northeast and upper Midwest of North America (Crum 1988; Gore 1983; Wheeler et al. 1983). From site to site, the diversity of both bryophyte and vascular peatland floras is highly influenced by the microhabitat heterogeneity of the peatland. The greater the diversity of microhabitats available, the greater the species richness of the peatland (Anderson and Davis 1997; Vitt et al. 1995).

An extensive and often confounding literature exists regarding the classification of peatland systems. Researchers classify peatlands utilizing a variety of terms and definitions that assess peatland attributes ranging from edaphic and physical characteristics to vegetation community composition (Gore 1983). Based on water chemistry, peatlands can be classified generally into two polar groups, ombrotrophic peatlands (bogs) and minerotrophic peatlands (fens). A third group, oligotrophic peatlands, have intermediate water chemistry and floristic characteristics.

Ombrotrophic peatlands receive all mineral subsidies from atmospheric deposition or from nutrients released during the slow decay of organic matter within the peatland basin. Thus, these peatlands are extremely nutrient-limited (Crum 1988; Damman and French 1987; Gore 1983). Ombrotrophic peatlands may be cut off from drainage or flushing by their geomorphological orientation, such as in a kettlehole bog. These peatlands may also be isolated from the water table by their own prolific deposition of peat that can elevate the peatland above the influence of groundwater, such as in a maritime raised bog (Crum 1988; Damman and French 1987). Due to the lack of active water circulation, hydrogen ions accumulate in ombrotrophic peatlands often resulting in pH values of 4.01–4.25 in the narrow definition of Gorham and Janssens (1992a), or less than 5.0 in the broader definition of Vitt et al. (1995). Bryophyte communities in ombrotrophic and oligotrophic peatlands are extensive and are dominated by *Sphagnum* species (Crum 1988; Gorham and Janssens 1992a; Janssens and Glaser 1986; Schwintzer 1981; Vitt 1990, Vitt and Slack 1975, 1984; Vitt et al. 1995).

Minerotrophic peatlands (fens) are relatively nutrient-rich compared to their ombrotrophic counterparts. Fens receive mineral subsidies from rheotrophic (flowing) ground or surface sources, as well as from precipitation. The nutritive input of a fen is unique from site to site based on the physical orientation and hydrology of the peatland. Thus, the mineral concentrations of fens are tremendously variable (Damman and French 1987; Gignac and Vitt 1994; Gore 1983). Edaphic inputs enrich fen peats with higher concentrations of calcium, iron, magnesium, aluminum, and phosphorus ions and higher relative pH levels than ombrotrophic peatlands (Gignac and Vitt 1994; Gorham 1990;

Jeglum 1971; Schwintzer 1978; van Breeman 1995). Fens are often subclassified as poor fens (pH 4–6) to extreme rich fens (pH 6–7.5) based on the relative minerotrophy, pH values, and plant species composition (pH values for the upper Midwest from Crum 1988).

The relative minerotrophy and higher pH levels of fens are reflected in their floras which become more species-rich along a gradient from low to high nutrient availability, i.e., oligotrophic to minerotrophic conditions (Crum 1988; Damman and French 1987; Glaser 1987; Gorham 1990; Schwintzer 1981). Fens typically have an extensive sedge cover that is often dominated by *Carex lasiocarpa* Ehrh., a less prominent bryophyte cover, and greater overall species richness compared to ombrotrophic peatlands (Crum 1988; Glaser 1987; Schwintzer 1978; Vitt et al. 1995).

Bryophytes in fens tend to be dominated by members of the Amblystegiaceae, including *Amblystegium* spp., *Calliergon* spp., and *Scorpidium scorpioides* (Hedw.) Limpr. (Gorham and Janssens 1992a; Janssens and Glaser 1986; Vitt 1990; Vitt et al. 1995). *Sphagnum* taxa have reduced frequencies in fen ecosystems, but are nevertheless present. Species such as *Sphagnum teres* (Schimp.) Ångstr. ex C. Hartm. and *Sphagnum subsecundum* Nees ex Sturm are typically prominent in alkaline fen conditions, particularly on the edge of the mat along open water (Crum 1988).

Most basin peatlands containing ponds or lakes exhibit the classic zonation of vegetation communities where a floating community of sedges, *Sphagnum,* and/or ericaceous shrubs encroach over the open water of a lake (e.g., Crow 1969; Dunlop 1987; Fahey 1993; Fahey and Crow 1995; Schwintzer and Williams 1974). The more or less concentric vegetation patterns of peatlands that radiate outward from lake margins led early ecologists to propose the "hydrosere model" of peatland succession. The hydrosere model states that lake margin communities fill in or terrestrialize the open water of a pond or lake, and initiate a successional sequence that passes through ericaceous shrub associations, coniferous forest associations, and finally culminates in an upland forest climax community on what was formerly the peatland (e.g., Dansereau and Segadas-Vianna 1952; Gates 1942; Transeau 1903).

Recently, this traditional hydrosere explanation that links spatial zonation with successional processes has been called into question by peatland ecologists (Klinger 1996; van Breeman 1995). Although the process of terrestrialization in basin peatlands has been well documented, Klinger (1996) has reservations regarding two major tenets of the hydrosere model. First, it is unlikely that a mesic forest "climax" is the ultimate successional destiny of a peatland basin. Second, terrestrialization of peatlands is not necessarily a unidirectional process; instead it is quite often a dynamic progression of vegetation advance and recession along a water body (e.g. Schwintzer and Williams 1974).

Citing a lack of data from stratigraphic, dendrochronological, and vegetational analyses to support strict hydrosere peatland succession, "the bog climax model" of peatland succession has been proposed (Klinger 1996). This model states that peatland conditions are their own climax in middle to high latitudes. In this model, peatland mats extend outward from lake margins via terrestrialization, while *Sphagnum* mosses along the outer edge of the peatland expand beyond the limits of the basin and into the upland via paludification. Therefore, in the absence of large scale disturbances and alterations of peatland hydrology, peatland systems remain ecologically intact for thousands of years (Klinger 1996). Early in peatland succession allogenic factors are important, but they later become secondary to autogenic factors that are initiated and maintained by the flora itself (Klinger 1996).

This paper outlines the vegetation associations found within Little Dollar Lake peatland based on field observations and TWINSPAN analysis. Comparisons of vegetation patterns at Little Dollar Lake peatland to other North American peatlands in the upper Midwest, Canada, and the Northeast are emphasized. The role of terrestrialization and paludification in peatland succession is also discussed with reference to vegetation patterns observed at Little Dollar Lake peatland.

## SITE DESCRIPTION

The Little Dollar Lake peatland basin is 14 hectares (34 acres) in area. The peatand is located in west-central Mackinac County on the eastern Upper Peninsula of Michigan (T44N, R8W, NE1/4 Sec. 28, Hudson Township). Little Dollar Lake has acidic water chemistry (mean pH = 4.5, n = 40) and is situated in a shallow glacial scour basin. Based on pollen stratigraphy and sedimenta-

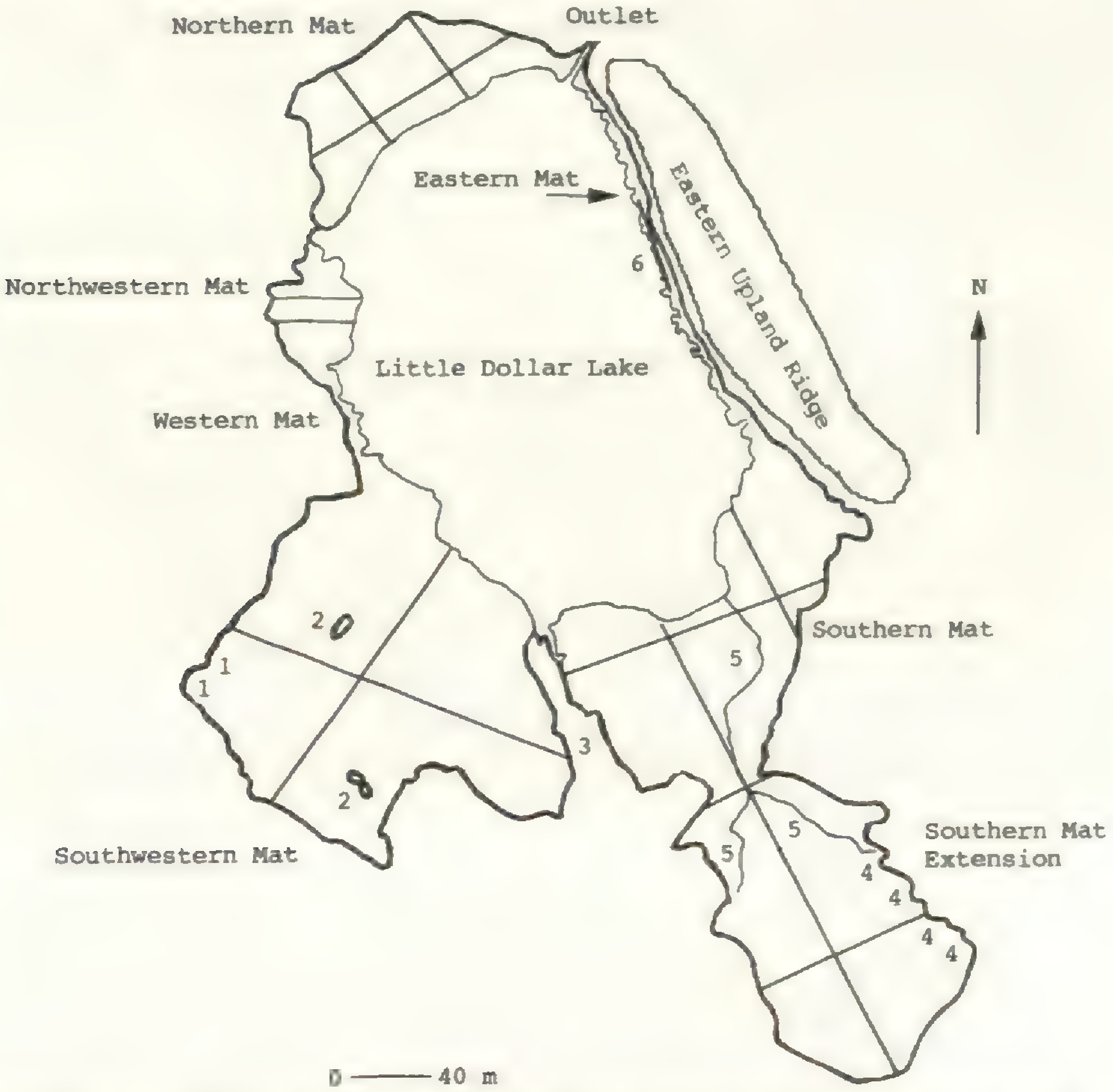
Northern Mat
Outlet
Eastern Mat
Eastern Upland Ridge
6
Northwestern Mat
N
Little Dollar Lake
Western Mat
2
Southern Mat
1
1
5
3
2
5
Southern Mat Extension
Southwestern Mat
5
4
4
4
4
0 40 m

Figure 1. Map of Little Dollar Lake peatland illustrating transect locations and selected features of local geography around and within the peatland basin. Scale is approximate. 1. *Typha* colony adjacent to the truck trail; 2. Upland islands on southwestern mat; 3. Upland peninsula; 4. Muck pools in the southern mat extension; 5. Stream channel; 6. Location of the transect on the eastern mat parallel to the upland.

tion, the peatland around Little Dollar Lake began to form approximately 3500 years before present as a result of prolonged increases in the regional water tables of eastern upper Michigan (Futyma 1982). Basin morphology, post-glacial history, soils, surrounding upland vegetation, and climate are described by Hellquist (1996) and Hellquist and Crow (1997).

Little Dollar Lake is surrounded by seven peatland mats of varying extent. These mats were named based on their compass-point position around Little Dollar Lake (Figure 1). Each mat is colonized by a variety of plant associations. In general, the peatland is characterized by a nearly continuous layer of *Sphagnum* spp. covered by expanses of open ericaceous scrub. A narrow, floating mat fringes much of the lakeshore and a graminoid lagg borders the upland of several mats.

## MATERIALS AND METHODS

**Bryophyte and vascular vegetation sampling.** Vegetation analysis and mapping were conducted using transect sampling procedures. Thirteen transects, intersecting as many plant communities as possible, were surveyed and divided into ten-meter intervals. Using a table of pseudo-random numbers, two one-meter-square (1 m × 1 m) quadrats were chosen for sampling within each ten-meter interval. In some spatially narrow habitats, extra quadrats were added to help insure adequate sampling. From July 12, 1995 through August 15, 1995, 279 one-meter-square quadrats were sampled visually for frequency and absolute percent cover of bryophyte and vascular species. Cover was defined as ". . . an estimate of the area of coverage of the foliage of the species in a vertical projection on to the ground" (Shimwell 1971, p. 110). Species composition and absolute percent cover were estimated separately for the bryophyte and vascular strata in each quadrat.

**TWINSPAN vegetation analysis.** Bryophyte and vascular percent cover data from the 279 sampled quadrats were analyzed using two-way indicator species analysis (TWINSPAN; Hill 1979). TWINSPAN is a polythetic divisive procedure that uses reciprocal averaging to ordinate quadrats, ultimately creating an ordered site-by-species two-way table (Hill 1979). Seven pseudospecies cut levels (Hill 1979; van Tongeraan 1987) were established as follows: 1 (0–1% cover), 2 (1–2% cover), 3 (2–5% cover), 4 (5–10% cover), 5 (10–25% cover), 6 (25–50% cover), and 7 (50–100% cover). All cut levels were weighted equally.

For studies involving the classification of ecological communities, there are several advantages to employing TWINSPAN analysis. These include its use of raw data, its hierarchical classification of both plots and species, and the ability to rewrite the arranged data matrix in a dendrogram format that enhances the clarity of plot relationships (Gauch 1982). TWINSPAN analysis has been utilized in many investigations of peatland vegetation

Table 1. Species richness of the four vegetation cover types (CT) and six cover phases (PHS). The number of quadrats in each cover type or phase is noted in parentheses.

| TWINSPAN Community Delineation | Species Richness |
|---|---|
| *Potamogeton confervoides–Utricularia geminiscapa* CT | 7 |
| *Calamagrostis canadensis* CT (27) | 54 |
| *Iris versicolor–Lycopus uniflorus* PHS (13) | 44 |
| *Sphagnum cuspidatum–Dulichium arundinaceum* PHS (14) | 30 |
| *Chamaedaphne calyculata* CT (220) | 56 |
| *Sphagnum recurvum–Carex oligosperma* PHS (186) | 53 |
| *Sphagnum magellanicum–Sarracenia purpurea* PHS (34) | 27 |
| *Chamaedaphne calyculata–Triadenum fraseri* CT (32) | 37 |
| *Sphagnum majus* PHS (22) | 26 |
| *Sphagnum papillosum* PHS (10) | 31 |

(Anderson and Davis 1997; Dunlop 1987; Fahey and Crow 1995; Miller 1996; Slack et al. 1980; Vitt and Chee 1990; Vitt et al. 1990).

## RESULTS

**TWINSPAN classification.** Field observations and data weighed in concert with TWINSPAN analysis resulted in the delineation of four distinct vegetation cover types (including the aquatic vegetation of the lake) and six constituent vegetation phases within the Little Dollar Lake basin (Table 1; Figures 2 and 3). The aquatic cover type was recognized based on field observations. Although these cover types were delineated primarily through TWINSPAN analysis, only plant communities that could be discerned clearly in the field have been recognized. The complete TWINSPAN two-way table and raw data are available in Hellquist (1996).

Those species that were prominent both in the field and in the TWINSPAN analysis were chosen as appropriate species to name the cover types (CT) and phases (PHS). Due to overlap of indicator species between clusters, or to the relatively inconspicuous nature of the TWINSPAN indicator species in the physiognomy of a cover type or phase, the TWINSPAN indicator species were not always adopted as appropriate "representative species" for the names of cover types and phases. Indicator species for the cover types and phases are noted in Tables 2–10. Although sim-

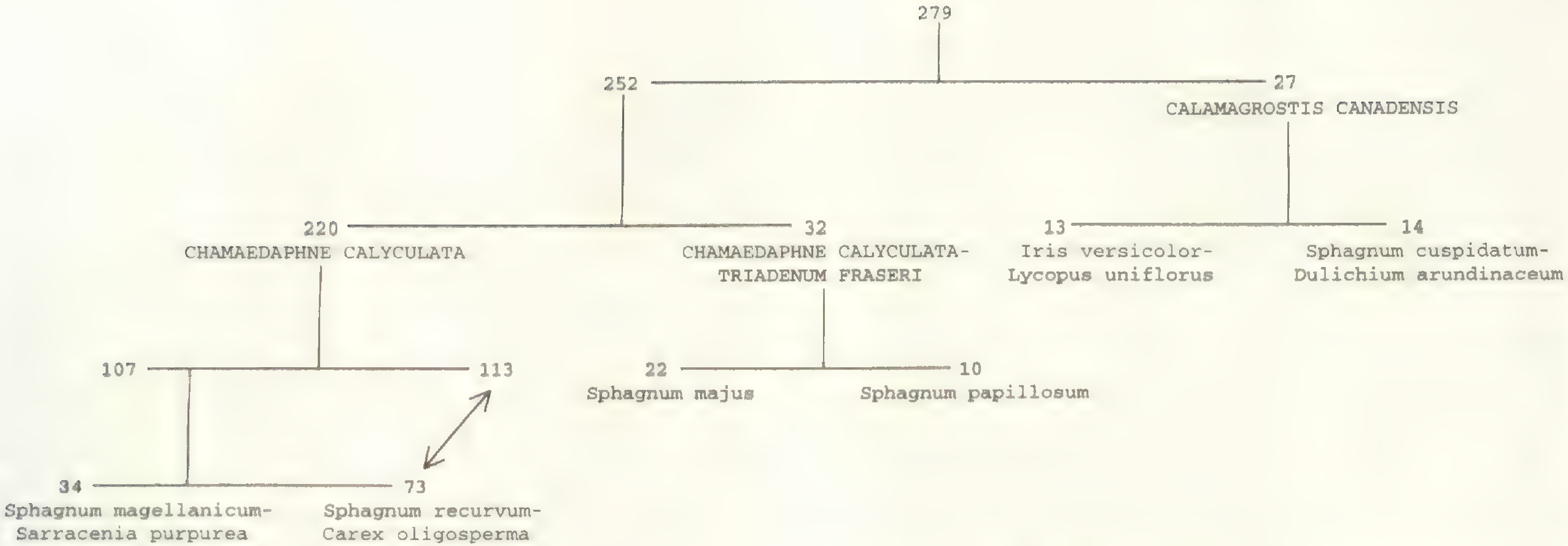
279
252
27
CALAMAGROSTIS CANADENSIS
220
CHAMAEDAPHNE CALYCULATA
32
CHAMAEDAPHNE CALYCULATA-
TRIADENUM FRASERI
13
Iris versicolor-
Lycopus uniflorus
14
Sphagnum cuspidatum-
Dulichium arundinaceum
107
113
22
Sphagnum majus
10
Sphagnum papillosum
34
Sphagnum magellanicum-
Sarracenia purpurea
73
Sphagnum recurvum-
Carex oligosperma

Figure 2. Dendrogram of the vegetation cover types and phases as delineated by TWINSPAN and field observation. Designations in all capital lettering are cover types, designations with capital and lowercase lettering are phases. Numbers refer to the number of quadrats in each cover type or phase. The arrow indicates that the clusters of 113 and 73 plots were combined to form the *Sphagnum recurvum–Carex oligosperma* phase.

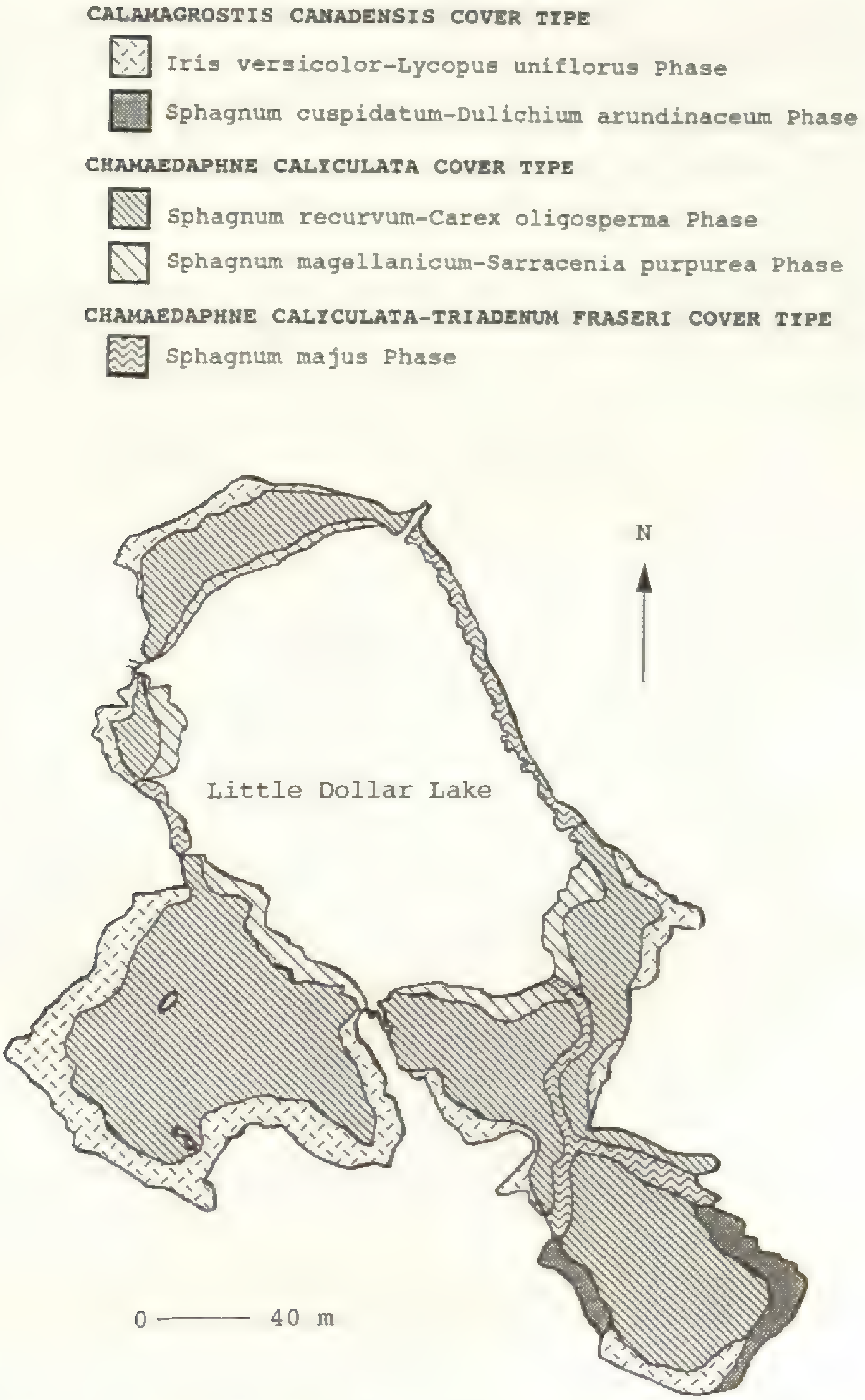
CALAMAGROSTIS CANADENSIS COVER TYPE
Iris versicolor-Lycopus uniflorus Phase
Sphagnum cuspidatum-Dulichium arundinaceum Phase
CHAMAEDAPHNE CALYCULATA COVER TYPE
Sphagnum recurvum-Carex oligosperma Phase
Sphagnum magellanicum-Sarracenia purpurea Phase
CHAMAEDAPHNE CALYCULATA-TRIADENUM FRASERI COVER TYPE
Sphagnum majus Phase
N
Little Dollar Lake
0 40 m

Figure 3. Vegetation map of Little Dollar Lake peatland illustrating the extent of the vegetation cover types and constituent vegetation phases. The *Sphagnum papillosum* phase is not mapped due to its narrow spatial distribution. This phase is present in a narrow (~1.0 m) band along the lake margin in all areas where the *Sphagnum magellanicum–Sarracenia purpurea* phase is present. Scale is approximate.

ilarities to other peatland complexes in the upper Midwest do exist, the names of these communities are not intended to have regional applicability due to the inherent variability of hydrology and topography that directly influences the composition of individual peatland floras.

TWINSPAN classification split the initial set of 279 quadrats into two groups, a group of 252 quadrats and a second group of 27 quadrats (Figure 2). The 27 quadrats were designated as the *Calamagrostis canadensis* CT. At the second level the *C. canadensis* CT was divided further into phases of 13 and 14 quadrats respectively. The cluster of 13 quadrats was named the *Iris versicolor–Lycopus uniflorus* PHS, and the cluster of 14 quadrats was named the *Sphagnum cuspidatum–Dulichium arundinaceum* PHS (Figure 2).

The remaining 252 quadrats were split into two clusters, one cluster of 220 quadrats and one cluster of 32 quadrats. The cluster of 220 quadrats was named the *Chamaedaphne calyculata* CT or "ericaceous scrub," and the cluster of 32 quadrats was named the *C. calyculata–Triadenum fraseri* CT (Figure 2). The two phases of the *C. calyculata* CT consisted of clusters of 186 quadrats and 34 quadrats.

TWINSPAN separated the 220 quadrats of the *Chamaedaphne calyculata* CT into clusters of 107 and 113 quadrats (Figure 2). The cluster of 113 quadrats at the third level had an essentially uniform species composition. In the field, this group of 113 quadrats was indistinguishable from the cluster of 73 quadrats at the fourth cut level. Therefore, the 73 remaining quadrats on the fourth cut level and the entire 113 quadrat dichotomy were combined into a cluster of 186 quadrats (Figure 2). These 186 quadrats were representative of the *Sphagnum recurvum–Carex oligosperma* PHS (hummock-hollow complex) of the *C. calyculata* CT.

The remaining 34 quadrats, isolated from TWINSPAN's cluster of 107 quadrats at the fourth level, had a unique suite of species that corresponded to the floating-mat community along the northern and southern lake margin. This cluster was named the *Sphagnum magellanicum–Sarracenia purpurea* PHS of the *Chamaedaphne calyculata* CT (Figure 2).

Lastly, at the second cut level, the cluster of 32 quadrats that composed the *Chamaedaphne calyculata–Triadenum fraseri* CT was divided into two constituent phases (Figure 2). The *Sphag-*

*num majus* PHS consisted of 22 quadrats and was associated with the stream channel and the narrow eastern and western mats (Figures 1 and 3). The remaining ten quadrats, the *Sphagnum papillosum* PHS, formed an approximately two to three meter zone immediately bordering the open water of the majority of the peatland.

**Species richness and frequency within sampling quadrats.** The *Calamagrostis canadensis* CT and the *Chamaedaphne calyculata* CT were the most species rich of the cover types (Table 1). The *C. canadensis* CT was restricted to more minerotrophic lagg areas. Despite being sampled by only 27 quadrats, this cover type contained 54 species. The *C. calyculata* CT was slightly more diverse, but was sampled extensively by 220 quadrats. The most diverse phase was the *Sphagnum recurvum–Carex oligosperma* PHS of the *C. calyculata* CT (Table 1). The next most diverse phase was the *Iris versicolor–Lycopus uniflorus* PHS of the *C. canadensis* CT (Table 1). The *I. versicolor–L. uniflorus* PHS consisted of only 13 quadrats but contained 44 different species. The most species-poor cover type or phase was the *Potamogeton confervoides–Utricularia geminiscapa* CT. With only seven species, this cover type was restricted to the open water of Little Dollar Lake.

The nutrient-poor nature of the peatland was emphasized by the dominance of the Sphagnaceae (peat moss family) and the Ericaceae (heath family) on a visual and a quantitative level within the 279 sampling quadrats. Of the ten most frequent species in the 279 quadrats, eight belonged to either the Sphagnaceae or the Ericaceae (Figure 4). Of these ten species, *Chamaedaphne calyculata* (L.) Moench was the most abundant species, occurring in 258 quadrats (92%). *Vaccinium oxycoccos* L. was second, occurring in 218 quadrats (78%). The most abundant sedge was *Carex oligosperma* Michx. which was present in 106 quadrats (38%).

The tenth most frequent taxon in the 279 quadrats was *Acer rubrum* L. This species was present only as seedlings or small saplings in the quadrats sampled. Seedlings were noted in 23% of the quadrats sampled. In every quadrat in which *A. rubrum* appeared, it had a cover value of less than 2%. Of the ten most abundant species, the only bryophytes were members of the Sphagnaceae (Figure 4).

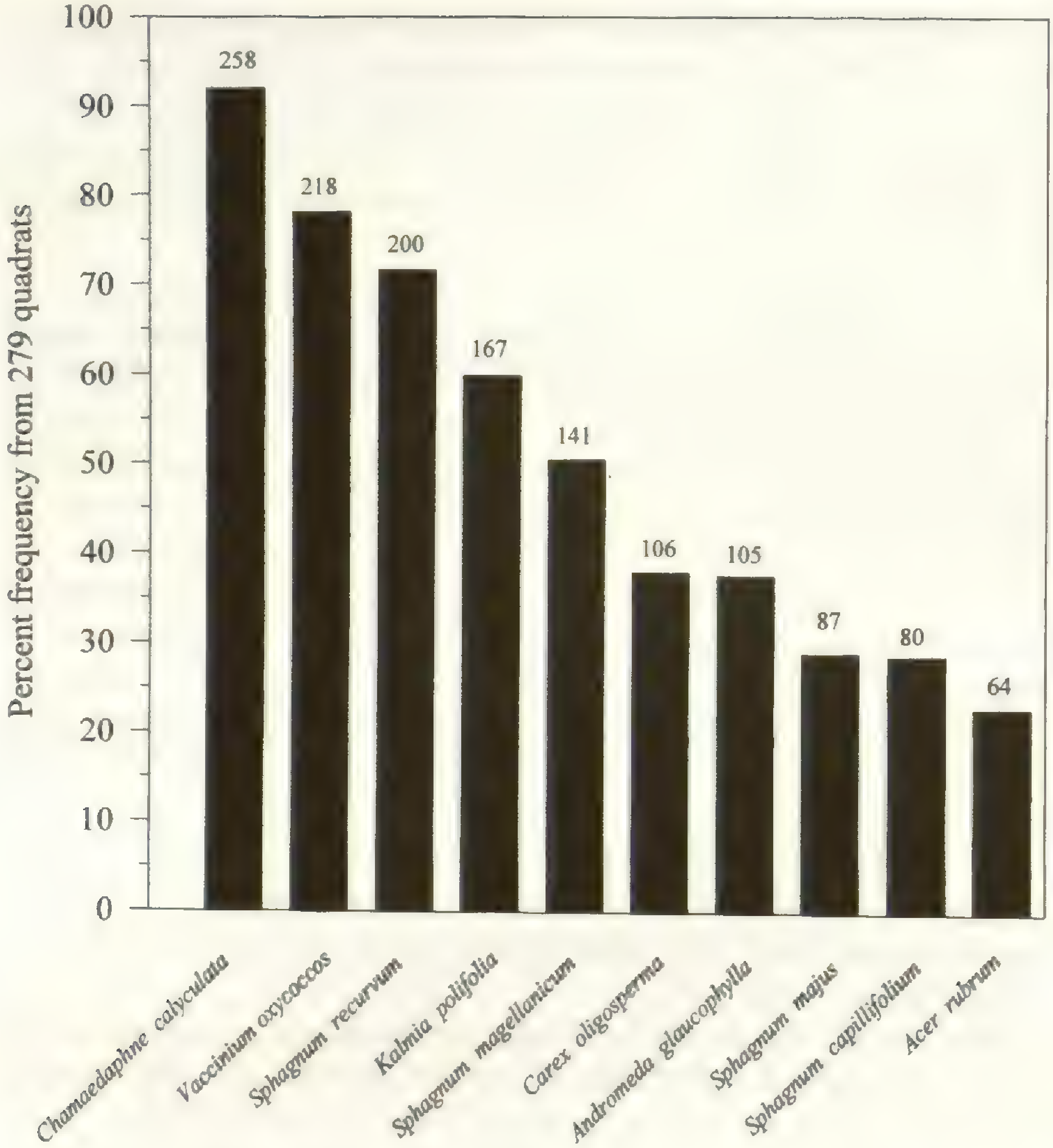

Figure 4. Percent frequency of the ten most abundant species in the 279 quadrats sampled. The number above each bar equals the total number of quadrats in which each species occurred.

## DISCUSSION

**The vegetation of Little Dollar Lake peatland.** The bryophyte flora of Little Dollar Lake peatland consisted of 36 species including eleven species of *Sphagnum*. The vascular flora of the peatland was comprised of 93 species dominated by sedge species (Cyperaceae) and heath species (Ericaceae). The complete bryophyte and vascular flora of Little Dollar Lake peatland, including comments on abundance and habitats, is presented in Hellquist and Crow (1997).

The following discussion summarizes the vegetation patterns at Little Dollar Lake peatland, and emphasizes the presence of various plant species as a means to infer the nutrient status of a peatland or microhabitats within a peatland. The four cover types and the six constituent phases are discussed in a roughly centripetal manner starting with the lagg communities on the outside of the peatland basin and proceeding inward toward Little Dollar Lake.

### 1. *Calamagrostis canadensis* Cover Type

The outermost portion of a basin peatland is known as the lagg or moat. The lagg is an ecotone (sensu Risser 1995) between the consolidated peat of the open mat and the mineral soils of the upland. The lagg is characterized by shallower, better aerated peat that is enriched by nutrients from the adjacent upland (Crum 1988; Damman and French 1987; Gore 1983). A moat of open water separating the upland from the peatland proper is often found within the lagg area. The lagg is typically one of the most botanically diverse communities within a peatland. The lagg usually contains minerotrophic wetland species that are not exclusively associated with peatland floras except in the context of lagg habitats (Crum 1988). Thus, the species composition of the lagg reflects a more minerotrophic or marsh-like physiognomy compared to the majority of the peatland basin.

The *Calamagrostis canadensis* CT formed an encircling, fen-like community adjacent to the upland on all peatland mats of the basin except the narrow eastern and western mats (Figure 3). In northern Michigan, a *C. canadensis* (Michx.) P. Beauv. association typically follows fire and sometimes develops in the marginal areas of peatlands that are damp, but not extremely wet (Gates 1942). In the summers of 1994 and 1995, this cover type was merely damp with no standing water. In 1996, however, most of this cover type was saturated with water or had standing water 0.25 to 0.50 m in depth, especially in areas of the southwestern mat and southern mat extension.

*Sphagnum* species were not as prominent in the *Calamagrostis canadensis* CT, with only *S. recurvum* P. Beauv. and *S. cuspidatum* Hoffm. occurring with some frequency (Table 2). *Sphagnum recurvum* was apparent in the open, outer areas of lagg closer to the ericaceous scrub, while *S. cuspidatum* formed lush pockets in the wettest, muckiest areas of the lagg. In 1996, *S. cuspidatum*

Table 2. Mean percent cover and percent frequency of dominant and associated species in the *Calamagrostis canadensis* cover type consisting of 27 quadrats out of 279. Species having less than 10% frequency are not included in the table. *TWINSPAN indicator species. *Lycopus uniflorus* was also designated as an indicator species, but does not appear in the table.

| | Mean % Cover | % Frequency |
|---|---|---|
| BRYOPHYTES | | |
| *Sphagnum recurvum* | 55 | 51.9 |
| *Sphagnum cuspidatum** | 27 | 30.0 |
| *Warnstorfia fluitans* | 5 | 14.8 |
| *Calliergon cordifolium* | 27 | 11.1 |
| *Calliergon stramineum* | 22 | 11.1 |
| *Callicladium haldanianum* | 4 | 11.1 |
| VASCULAR PLANTS | | |
| *Calamagrostis canadensis** | 30 | 88.9 |
| *Carex lasiocarpa* | 38 | 74.1 |
| *Potentilla palustris* | 5 | 55.6 |
| *Triadenum fraseri* | 2 | 44.4 |
| *Chamaedaphne calyculata* | 18 | 37.0 |
| *Acer rubrum* | <1 | 37.0 |
| *Lysimachia thyrsiflora* | 2 | 30.0 |
| *Iris versicolor** | 14 | 26.0 |
| *Glyceria canadensis* | 26 | 18.5 |
| *Lysimachia terrestris* | 2 | 18.5 |
| *Galium trifidum* | 3 | 15.0 |
| *Dulichium arundinaceum* | 20 | 14.8 |
| *Impatiens capensis* | 8 | 14.8 |
| *Carex oligosperma* | 10 | 11.1 |
| *Scutellaria galericulata* | 5 | 11.1 |
| *Equisetum fluviatile* | 2 | 11.1 |

flourished in the standing water of southern lagg areas with delicate individuals growing to lengths as long as 0.25 m. While there was a lack of *Sphagnum* diversity in this cover type, members of the Amblystegiaceae contributed to the diverse bryophyte flora of this cover type. Members of this minerotrophic-indicative family, *Calliergon cordifolium* (Hedw.) Kindb. and *C. stramineum* (Brid.) Kindb., often were observed thriving in wet, decomposing leaf litter.

The two most frequent and dominant vascular species were *Calamagrostis canadensis* and *Carex lasiocarpa* (Table 2). These two species grew intermingled and gave the lagg community its narrow-leaved graminoid texture that was readily distinguished from the neighboring ericaceous scrub community. At the height of the growing season, the prominence of *C. canadensis* gave the lagg a distinct marsh-like appearance. Other widely scattered, but locally abundant species of this community type included *Galium tinctorium* L., *Iris versicolor* L., *Lysimachia thyrsiflora* L., *L. terrestris* (L.) B.S.P., *Lycopus uniflorus* Michx., and *Potentilla palustris* (L.) Scop.

The species within the graminoid lagg at Little Dollar Lake peatland were similar to the herbaceous component of the lagg at Mud Pond Bog (Moultonborough, NH). Species found in both of these peatlands included *Calamagrostis canadensis, Lycopus uniflorus, Scirpus cyperinus* (L.) Kunth, and *Scutellaria galericulata* L. (C. E. Hellquist, ms. in prep.). The lagg communities at Mud Pond Bog were also characterized by an extensive tall shrub lagg association dominated by *Ilex verticillata* (L.) A. Gray, *Nemopanthus mucronatus* (L.) Trel., *Lyonia ligustrina* (L.) DC., *Vaccinium corymbosum* L., and *Viburnum nudum* L. (C. E. Hellquist, ms. in prep.). At Little Dollar Lake, typical lagg shrubs such as *I. verticillata* and *N. mucronatus* grew infrequently within the peatland basin itself, although both taxa grew abundantly in rich upland soils that immediately fringed the lagg. The presence of *I. verticillata, N. mucronatus,* and *V. nudum* var. *cassinoides* (L.) T. & G. at Little Dollar Lake is reminiscent of the *I. verticillata–N. mucronatus* community type described for northern Michigan kettlehole peatlands (Vitt and Slack 1975). This cover type also resembled the *I. verticillata–Acer–Carex canescens* community type found nearest the upland in Mud Pond Bog (Hillsborough, NH; Dunlop 1987). Species common to these cover types include *I. verticillata, Acer rubrum, Lysimachia terrestris, Lycopus uniflorus,* and *C. canadensis* (Dunlop 1987).

### 1A. *Iris versicolor–Lycopus uniflorus* Phase

The substrate of the *Iris versicolor–Lycopus uniflorus* PHS (Figure 3) was composed of very shallow peat (<1.0 m) that often was covered by decaying leaf duff from upland trees. The presence of shade-tolerant *Sphagnum squarrosum* Crome emphasized the nutrient-rich nature of the lagg habitat. *Sphagnum squarrosum* typically grows in minerotrophic, alkaline *Thuja occidentalis* L. swamps and swampy woodlands (Andrus 1980; Crum 1983, 1988). The most abundant non-*Sphagnum* bryophyte was *Calliergon cordifolium,* a species that thrived in damp leaf

Table 3. Mean percent cover and percent frequency of dominant and associated species in the *Iris versicolor–Lycopus uniflorus* phase of the *Calamagrostis canadensis* cover type (13 quadrats). Species having less than 10% frequency are not included in the table. *TWINSPAN indicator species.

| | Mean % Cover | % Frequency |
|---|---|---|
| BRYOPHYTES | | |
| *Sphagnum recurvum* | 60 | 84.6 |
| *Warnstorfia fluitans* | 3 | 15.4 |
| *Calliergon cordifolium** | 27 | 23.1 |
| *Callicladium haldanianum* | 4 | 23.1 |
| *Drepanocladus uncinatus* | 6 | 15.4 |
| *Dicranum flagellare* | 7 | 15.4 |
| *Pleurozium schreberi* | 8 | 15.4 |
| VASCULAR PLANTS | | |
| *Calamagrostis canadensis* | 44 | 100.0 |
| *Carex lasiocarpa* | 31 | 69.2 |
| *Potentilla palustris* | 4 | 61.5 |
| *Lycopus uniflorus* | 7 | 61.5 |
| *Iris versicolor* | 14 | 53.8 |
| *Acer rubrum* | <1 | 53.8 |
| *Triadenum fraseri* | 3 | 53.8 |
| *Lysimachia terrestris* | 2 | 38.5 |
| *Impatiens capensis* | 8 | 30.8 |
| *Galium trifidum* | 3 | 30.8 |
| *Chamaedaphne calyculata* | 6 | 23.1 |
| *Scutellaria galericulata* | 5 | 23.1 |
| *Carex canescens* | 8 | 15.4 |
| *Carex oligosperma* | 13 | 15.4 |
| *Viola macloskeyi* | 6 | 15.4 |

litter with *Warnstorfia fluitans* (Hedw.) Loeske [*Drepanocladus fluitans* (Hedw.) Warnst.]. Several bryophyte taxa were restricted to this phase including the leafy liverworts *Chiloscyphus polyanthos* (L.) Corda and *Lophocolea heterophylla* (Schrad.) Dum., as well as the mosses *Climacium dendroides* (Hedw.) Web. & Mohr. and *Plagiothecium denticulatum* (Hedw.) Schimp. in B.S.G.

Dominant vascular species included the same suite of species that defined the graminoid lagg cover type as a whole (*Calamagrostis canadensis, Carex lasiocarpa,* and *Iris versicolor*; Table 3). The prominence of *I. versicolor* and *Lysimachia terrestris* made this phase readily apparent in the field. Northern Michigan peatlands may have a fringing *Iris* association less than a meter wide (Gates 1942). At Little Dollar Lake, *I. versicolor* was a prominent component of the *C. canadensis* CT with a distribution several meters in width, especially in the lagg areas of the southern-oriented peatland mats.

Within the *Iris versicolor–Lycopus uniflorus* PHS there was one locality that had an entirely unique species composition compared to the rest of the peatland. This area was situated within the lagg of the southwestern mat (Figure 1) in an area that apparently was influenced by runoff from a seasonal, dirt truck trail (Hellquist 1996). In this area, *Typha latifolia* L. was well established. Futyma (1982) noted the presence of *Typha* in the basin in the early 1980s, but made no reference to the location of the colony. Other species essentially limited to this distinct lagg habitat were *Carex stipata* Muhl., *Epilobium ciliatum* Raf., *Polygonum cilinode* Michx., *Rubus canadensis* L., *Scutellaria lateriflora* L., and *Rumex obtusifolius* L.

### 1B. *Sphagnum cuspidatum–Dulichium arundinaceum* Phase

The *Sphagnum cuspidatum–Dulichium arundinaceum* PHS occurred in two distinct areas in the southeastern and western lagg areas of the southern mat extension (Figure 3). This association was apparent in the wettest areas of lagg that contained exposed, mucky peat. In 1996, this area was covered by standing water roughly 0.25 to 0.50 m deep. The most frequent vascular species of this phase included *Calamagrostis canadensis, Carex lasiocarpa, Chamaedaphne calyculata,* and *Potentilla palustris.* Thirteen species with greater than 10% frequency were present including *Glyceria canadensis* (Michx.) Trin., *Carex utriculata* F. Boott, *Equisetum fluviatile* L., and *Salix pedicellaris* Pursh (Table 4).

The dominant peat mosses of this phase were *Sphagnum recurvum* and *S. cuspidatum* (Table 4). Other important bryophyte species included members of the Amblystegiaceae such as *Warnstorfia fluitans, W. exannulata* (Schimp. in B.S.G.) Loeske [*Drepanocladus exannulatus* (Schimp. in B.S.G.) Warnst.], *Calliergon cordifolium,* and *C. stramineum.* Despite its infrequency in the quantitative sampling of this phase, *W. exannulata* formed an almost homogeneous bryophyte cover on exposed, mucky peat in the southeastern lagg of the southern mat extension. In 1996, this same population of *W. exannulata* was still vigorous despite being submerged in standing water. *Warnstorfia exannulata* is considered a dominant species of poor fens in Alberta along with *Sphagnum angustifolium* (C. Jens. ex Russ.) C. Jens., *S. majus*

Table 4. Mean percent cover and percent frequency of dominant and associated species in the *Sphagnum cuspidatum–Dulichium arundinaceum* phase of the *Calamagrostis canadensis* cover type (14 quadrats). Species having less than 10% frequency are not included in the table. *TWINSPAN indicator species.

| | Mean % Cover | % Frequency |
|---|---|---|
| BRYOPHYTES | | |
| *Sphagnum recurvum* | 38 | 21.4 |
| *Sphagnum cuspidatum** | 27 | 57.1 |
| *Warnstorfia fluitans* | 8 | 14.3 |
| *Sphagnum majus* | <1 | 14.3 |
| *Calliergon stramineum* | 30 | 14.3 |
| *Calliergon cordifolium* | 27 | 11.1 |
| VASCULAR PLANTS | | |
| *Calamagrostis canadensis** | 14 | 78.6 |
| *Carex lasiocarpa** | 43 | 78.6 |
| *Chamaedaphne calyculata* | 24 | 50.0 |
| *Potentilla palustris* | 5 | 50.0 |
| *Lysimachia thyrsiflora** | 1 | 35.7 |
| *Triadenum fraseri* | <1 | 35.7 |
| *Glyceria canadensis* | 32 | 28.6 |
| *Dulichium arundinaceum** | 20 | 28.6 |
| *Acer rubrum* | <1 | 21.4 |
| *Carex utriculata* | 8 | 14.3 |
| *Vaccinium macrocarpon* | 3 | 14.3 |
| *Equisetum fluviatile* | 2 | 14.3 |
| *Salix pedicellaris* | 23 | 14.3 |

(Russ.) C. Jens., and *S. jensenii* H. Lindb. (Vitt and Chee 1990). Although members of the Amblystegiaceae tend to prefer more minerotrophic microhabitats, *W. fluitans* and *C. stramineum* seem to occur in acid to intermediate acid habitats (ca. pH 3.7–6.0; Gorham and Janssens 1992b).

At Little Dollar Lake, several emergent vascular species colonized this rich muck including *Carex lasiocarpa, Dulichium arundinaceum* (L.) Britton, *Glyceria borealis* (Nash) Batchelder, *Juncus alpinus* Vill., *Potentilla palustris,* and *Puccinellia pallida* (Torr.) R. T. Clausen. The only locality of *Carex chordorrhiza* L. f. was in the exposed peat of the southeastern lagg. *Carex chordorrhiza* is considered a species indicative of poor fens in Minnesota (Wheeler et al. 1983) and rich fen conditions in Alberta (Vitt and Chee 1990).

Table 5. Mean percent cover and percent frequency of dominant and associated species in the *Chamaedaphne calyculata* cover type (220 quadrats). Species having less than 10% frequency are not included in the table. *TWINSPAN indicator species.

| | Mean % Cover | % Frequency |
|---|---|---|
| BRYOPHYTES | | |
| *Sphagnum recurvum* | 74 | 83.2 |
| *Sphagnum majus* | 50 | 36.3 |
| *Sphagnum magellanicum** | 14 | 26.5 |
| *Aulocomnium palustre* | 6 | 13.3 |
| *Sphagnum capillifolium** | 18 | 10.6 |
| VASCULAR SPECIES | | |
| *Chamaedaphne calyculata* | 46 | 99.1 |
| *Carex oligosperma* | 26 | 94.7 |
| *Kalmia polifolia* | 15 | 62.8 |
| *Andromeda glaucophylla* | 11 | 36.3 |
| *Acer rubrum* | <1 | 27.4 |
| *Vaccinium oxycoccos** | 7 | 14.2 |

### 2. *Chamaedaphne calyculata* Cover Type

The *Chamaedaphne calyculata* CT was unquestionably the most prominent cover type within the peatland (Figure 3). Members of the Ericaceae lent this cover type its scrubby, homogeneous appearance. These shrubs occurred more or less continuously across a mosaic of hummocks and hollows carpeted by several species of *Sphagnum*. The *Sphagnum recurvum–Carex oligosperma* PHS was characterized by the grounded hummock-hollow complex. The *Sphagnum magellanicum–Sarracenia purpurea* PHS formed narrow bands of quaking mat that fringed the majority of the lake (Figure 3).

The three dominant ericaceous shrubs of this cover type were *Chamaedaphne calyculata, Kalmia polifolia* Wangenh., and *Andromeda glaucophylla* Link (Table 5). The prostrate ericad *Vaccinium oxycoccos* was also apparent in this community, with individuals winding over *Sphagnum* and between branches of ericaceous shrubs on relatively open hummocks. *Carex oligosperma,* the most ubiquitous sedge of the peatland, was also characteristic of this cover type.

In northern Michigan, the *Chamaedaphne calyculata* association is the most ubiquitous in the region and is found extensively in almost every peatland (Gates 1942). *Andromeda glaucophylla,* *Kalmia polifolia, Ledum groenlandicum* Oeder, and *Vaccinium oxycoccos* are considered secondary components of the association (Gates 1942). All of the heath species at Little Dollar Lake, with the exception of *L. groenlandicum,* were readily apparent in the *C. calyculata* CT. At Little Dollar Lake, *L. groenlandicum* was scattered widely across the ericaceous scrub and was restricted to large, dry hummocks.

Schwintzer (1981) noted that "bogs" (i.e. poor fens) in northern Michigan were often dominated by ericaceous shrubs and *Sphagnum* spp. and suggested that their dominance in these habitats was due to reduced rheotrophic conditions in these peatlands. Vitt and Slack (1975) found that *Chamaedaphne calyculata* had wide habitat preferences and therefore was not directly linked to any discrete association of *Sphagnum* species. In the Northeast, the *C. calyculata* association is affiliated with oligotrophic to ombrotrophic sites under very wet conditions (Damman and French 1987). The dominance of *C. calyculata* in large expanses of peatland has been noted by many investigators (e.g. Crow 1969; Dunlop 1987; Fahey 1993; Fahey and Crow 1995; Schwintzer 1981; Vitt and Bayley 1984; Vitt and Slack 1975).

The *Chamaedaphne calyculata* CT at Little Dollar Lake resembled the "closed mat zone" of Vitt and Slack (1975) that was present in all eight of their northern Michigan study sites. This zone was distinguished by the presence of a tree layer of varying extent as well as an extensively developed ericaceous shrub layer (Vitt and Slack 1975). There was no tree canopy or evergreen parkland at Little Dollar Lake, despite the presence of several coniferous tree species including *Picea mariana* (Miller) B.S.P., *Abies balsamea* (L.) Miller, *Pinus strobus* L., and *Larix laricina* (Duroi) K. Koch that were widely dispersed on the peatland mat. *Picea mariana* and *L. laricina* become abundant in peatlands with low water tables and well-drained peats (Glaser 1987). The reduced prominence of these species at Little Dollar Lake may be indicative of a high water table.

The most abundant conifer in this cover type was *Pinus strobus,* represented by both saplings and several mature trees growing on the mat. Although *P. strobus* is not regarded as a wetland tree, this species is often found within peatlands (e.g. Crow 1969; Dunlop 1987; Fahey and Crow 1995; Miller 1996; Schwintzer 1981; C. E. Hellquist, ms. in prep.). In peatlands, *P. strobus* often grows to mature heights of several meters, but these individuals typically are unhealthy and chlorotic (Miller 1996; C. E. Hellquist, pers. obs.).

2A. *Sphagnum recurvum–Carex oligosperma* Phase

This phase occupied expanses of grounded mat that exhibited the undulating topography characterized by *Sphagnum* hummocks that rise up to a meter above shallow, trough-like hollows (Figure 3). The species composition of the hummock-hollow complex is maintained in part by the growth and autogenic successional trends of *Sphagnum* species. *Sphagnum* grows apically over individuals so that their stems build up a microtopography of undulating mounds (hummocks) that are supported by a scaffolding formed by the roots and branches of vascular plant species, especially ericaceous shrubs (van Breeman 1995; Vitt et al. 1975).

A highly overlapping, directional succession of *Sphagnum* taxa occurs along the hummock-hollow gradient (Andrus 1986; Andrus et al. 1983; Crum 1988; Horton et al. 1979; Vitt and Slack 1984; Vitt et al. 1975). *Sphagnum* species characteristic of hummocks have high water-storing capacity, greater capillary pull, higher productivity under nutrient-deficient conditions, a greater cation exchange capacity due to the higher quantities of polyurionic acids produced during growth, and an ability to inhabit self-maintained low pH microhabitats (Clymo and Hayward 1982; Moore and Bellamy 1974; Rydin 1985; Spearing 1972; van Breeman 1995; Vitt et al. 1975).

Due to the nutrient-poor nature of this cover type, the vegetation was dominated by *Sphagnum* species including *S. majus, S. recurvum, S. magellanicum* Brid., and *S. capillifolium* (Ehrh.) Hedw. Ericaceous species including *Chamaedaphne calyculata, Kalmia polifolia, Andromeda glaucophylla,* and *Vaccinium oxycoccos,* as well as *Carex oligosperma* were the other ubiquitous species of this cover type (Table 6). The four *Sphagnum* species are most abundant at the acid end of the pH spectrum from approximately pH 3.7 to 5.0 (Gorham and Janssens 1992b). The prominence of *C. calyculata, C. oligosperma,* and *Sphagnum* spp. in open oligotrophic mats is a frequent association in northern Michigan (Schwintzer 1981).

Hollows are depressed areas where the water table typically pools at or just below the surface, often forming a waterlogged trough. These niches tend to have more plentiful nutrient supplies and higher pH values than hummocks (Crow 1969; Crum 1988;

Table 6. Mean percent cover and percent frequency of dominant and associated species in the *Sphagnum recurvum–Carex oligosperma* phase of the *Chamaedaphne calyculata* cover type (186 quadrats). Species having less than 10% frequency are not included in the table. *TWINSPAN indicator species. *Sphagnum fuscum* and *Drosera rotundifolia* also were designated as indicator species for the 73 quadrat cluster of this cover type but do not appear in the table.

| | Mean % Cover | % Frequency |
|---|---|---|
| BRYOPHYTES | | |
| *Sphagnum recurvum** | 58 | 85.5 |
| *Sphagnum magellanicum* | 34 | 53.8 |
| *Sphagnum capillifolium* | 22 | 29.0 |
| *Sphagnum majus** | 47 | 25.8 |
| *Aulocomnium palustre* | 4 | 16.7 |
| VASCULAR SPECIES | | |
| *Chamaedaphne calyculata* | 42 | 98.8 |
| *Carex oligosperma* | 22 | 93.5 |
| *Kalmia polifolia* | 17 | 71.5 |
| *Andromeda glaucophylla** | 15 | 43.0 |
| *Vaccinium oxycoccos** | 25 | 39.2 |
| *Acer rubrum* | <1 | 25.3 |

Moore and Bellamy 1974; Vitt and Slack 1975; Vitt et al. 1975). *Sphagnum* species that inhabit hollows have a loose, flimsy appearance. These taxa are characterized by sparser and more elongate pendant branches, less efficient water retention and capillary pull, and a reduced production of polyuronic acids (Crum 1988; Moore and Bellamy 1974; Rice and Scheupp 1995; Rydin 1985; Spearing 1972; van Breeman 1995). These features may have been evolutionarily derived as a means to minimize resistance to gas exchange, therefore increasing the carbon assimilating capabilities of the aquatic *Sphagnum* species (Rice and Scheupp 1995).

The hummock-hollow bryophyte zonation at Little Dollar Lake followed a more or less typical sequence described for oligotrophic peatlands in northern Michigan (Crum 1988; Vitt et al. 1975) and Minnesota (Wheeler et al. 1983). From a hollow to the top of a hummock, the general sequence of *Sphagnum* species at Little Dollar Lake was *S. majus, S. recurvum, S. magellanicum, S. papillosum* Lindb., *S. capillifolium,* and *S. fuscum* (Schimp.) Klingrr.

*Sphagnum majus* inhabited the lowest, dampest troughs of the scrub, and is a species that may grow submerged or emergent. It is characteristic of hollows in open sedge mats and low areas in open laggs (Crum 1983). Frequently found with *S. majus* in saturated hollows was the moss *Warnstorfia fluitans,* and two liverworts, the relatively abundant *Cladopodiella fluitans* (Nees) Joerg., and the more scarce and minute *Cephaloziella elachista* (Jack) Schiffn. *Cladopodiella fluitans* is typically found in sunken microhabitats (e.g. deer trails) where water may accumulate (Crum 1988). At Little Dollar Lake, both of these leafy liverwort species grew in similar microhabitats and were primarily found interwoven among moist *Sphagnum* stems.

*Sphagnum recurvum* was abundant along the upper edges of the hollows. Colonies of *S. recurvum* usually blended into *S. magellanicum* and *S. capillifolium* along the sides of hummocks. *Sphagnum recurvum* is known to form "loose" carpets in the Great Lakes region (Crum 1983, 1988; Vitt et al. 1975). *Sphagnum recurvum* is abundant in mesotrophic microhabitats such as hollows in open peatland mats (Crum 1983), and thrives under acidic conditions with low calcium and magnesium concentrations (Vitt and Slack 1975). *Sphagnum recurvum* also has been noted as the dominant peat moss in some Ohio peatlands (Andreas and Bryan 1990). In New York, *S. recurvum* is considered to be indicative of "weakly minerotrophic" conditions and is found in poor fen habitats (Andrus 1980).

Growing among *Sphagnum majus* and *S. recurvum* was *Carex oligosperma,* the most abundant sedge in the peatland. *Carex oligosperma* inhabited open hollows throughout the grounded mat and is abundant in acidic northern Michigan basin peatlands (Vitt and Slack 1975). The presence of *Chamaedaphne calyculata* and *C. oligosperma* has been associated with oligotrophic nutrient regimes (Vitt and Bayley 1984). In the Red Lake peatland of Minnesota, heliophilous *C. oligosperma* is a dominant species of open ombrotrophic and poor fen habitats within boreal patterned peatlands (Glaser 1987; Wheeler et al. 1983). Common species that occur with *C. oligosperma* at Red Lake peatland are identical to species found at Little Dollar Lake including *Andromeda glaucophylla, C. calyculata, Eriophorum vaginatum* L. [*E. spissum* Fern.], *Kalmia polifolia, Ledum groenlandicum,* and *Vaccinium oxycoccos* (Wheeler et al. 1983). In Maine, similar communities dominated by *S. recurvum, S. magellanicum, C. oligosperma,* and

*C. calyculata* have been delineated over wide ranges of minerotrophic conditions (Anderson and Davis 1997).

At Little Dollar Lake, as elevation along the microtopographical gradient increased, *Sphagnum recurvum* abundance dwindled and *S. magellanicum* became prominent. This same pattern has been observed in other northern Michigan peatlands (Vitt and Slack 1975; Vitt et al. 1975). In some areas of Little Dollar Lake peatland, *S. papillosum* had a patchy distribution among *S. magellanicum* on low hummocks or on the sides of taller hummocks. *Warnstorfia fluitans,* a widespread northern moss species often found in acidic to moderately acidic conditions (Crum 1983; Janssens and Glaser 1986), also tended to inhabit moist nooks on the sides or bases of hummocks.

Near the tops of hummocks *Sphagnum magellanicum* faded out of prominence and blended into compact colonies of *S. capillifolium. Sphagnum magellanicum* and *S. capillifolium* are typical of poor fen (oligotrophic) mat habitats (Andrus 1980; Crum 1983, 1988). *Sphagnum magellanicum* and *S. capillifolium* are known to initiate hummocks and grow on the sides or tops of low hummocks (Crum 1983, 1988; Vitt and Slack 1975). *Sphagnum magellanicum* has an especially wide ecological amplitude across the hummock-hollow complex (Vitt and Slack 1975; Vitt et al. 1975).

Hummock tops are generally considered the driest, most nutrient depleted, and most acidic microhabitats along the hummock-hollow sequence (Andrus 1986; Crum 1988; Vitt et al. 1975). The tallest hummocks at Little Dollar Lake often were crowned with compact populations of *Sphagnum fuscum. Sphagnum fuscum* is frequently found on hummock tops (Vitt et al. 1975). *Sphagnum fuscum* is typical of open acid peatland habitats and is strongly indicative of oligotrophic conditions (Crum 1983) as well as "ombrotrophic to weakly minerotrophic" conditions (Andrus 1986). Often intermingled with *S. fuscum* on larger hummocks were *Polytrichum strictum* Brid. [*P. juniperinum* Hedw. var. *affine* (Funck) Brid.], *Calliergon stramineum, Dicranum undulatum* Brid., *Aulocomnium palustre* (Hedw.) Schwaegr., and *Bryum capillare* Hedw. *Polytrichum strictum* is associated with dry, oligotrophic hummock tops (Andrus et al. 1983; Crum 1983; Janssens and Glaser 1986; Vitt 1990; Vitt et al. 1975). *Calliergon stramineum* prefers damp microhabitats in bogs and fens (Crum 1983) and can inhabit acidic to moderately acidic conditions

(Gorham and Janssens 1992b). *Dicranum undulatum* is typically found in open peatland habitats especially on hummocks (Crum 1983).

An additional factor influencing the vegetation dynamics in this cover type was the presence of the caterpillars of the Chain-Spotted Geometer (*Cingilia catenaria* Drury, Lepidoptera: Geometridae), a pale white-colored moth whose caterpillars fed voraciously on ericaceous shrubs on the southwestern and southern mats of Little Dollar Lake peatland. This caterpillar is known to be an occasional pest on blueberry crops and has infested Ontario peatlands, often with severe consequences (McGuffin 1987; Reader 1979). Despite the wide-ranging feeding preferences reported for the Chain-Spotted Geometer (Franklin 1948; McGuffin 1987), at Little Dollar Lake it was observed specifically defoliating *Chamaedaphne calyculata, Kalmia polifolia,* and *Andromeda glaucophylla* (see Hellquist 1996 for further details of the Little Dollar Lake infestations).

### 2B. *Sphagnum magellanicum–Sarracenia purpurea* Phase

The *Sphagnum magellanicum–Sarracenia purpurea* PHS formed the relatively stable floating mat that was present within five to twenty meters of the lake margin on all mats except the eastern and western mats (Figure 3). This quaking mat was situated between the lake margin and the grounded mat and was easily distinguished by level expanses of peat mosses ("*Sphagnum* lawns"). The *Sphagnum* lawns at Little Dollar Lake were best developed along the lake margin on the northwestern, southwestern, and southern mats (Figure 3). These lawns had a gently undulating topography that was formed primarily by carpets of *S. magellanicum, S. capillifolium,* and *S. papillosum.* The lawn itself had the consistency of a saturated sponge, and was covered by sprigs of ericaceous shrubs, especially *Chamaedaphne calyculata* and *Kalmia polifolia* (Table 7). The height differential of the low sprig-like ericads of the *Sphagnum* lawn and waist-high shrubby ericads on the grounded mat was conspicuous.

*Sarracenia purpurea* L., *Scheuchzeria palustris* L., and *Eriophorum virginicum* L. thrived on the *Sphagnum* lawn where these species obtained their greatest prominence. In Ontario, where *Chamaedaphne calyculata* was less prominent, oligotrophic indicator species such as *Scheuchzeria palustris, Eriophorum* spp. and bryophytes including *Cladopodiella fluitans, Sphagnum ma-*

Table 7. Mean percent cover and percent frequency of dominant and associated species in the *Sphagnum magellanicum–Sarracenia purpurea* phase of the *Chamaedaphne calyculata* cover type (34 quadrats). Species having less than 10% frequency are not included in the table. *TWINSPAN indicator species.

| | Mean % Cover | % Frequency |
|---|---|---|
| BRYOPHYTES | | |
| *Sphagnum magellanicum* | 31 | 100.0 |
| *Sphagnum capillifolium* | 30 | 64.7 |
| *Sphagnum majus** | 28 | 58.8 |
| *Sphagnum papillosum* | 30 | 55.9 |
| *Sphagnum recurvum* | 20 | 38.2 |
| *Cladopodiella fluitans* | 4 | 23.5 |
| *Sphagnum cuspidatum* | 18 | 5.9 |
| VASCULAR PLANTS | | |
| *Chamaedaphne calyculata* | 23 | 100.0 |
| *Kalmia polifolia* | 14 | 91.2 |
| *Vaccinium oxycoccos* | 23 | 88.2 |
| *Carex oligosperma* | 20 | 88.2 |
| *Andromeda glaucophylla* | 8 | 67.6 |
| *Sarracenia purpurea** | 10 | 52.9 |
| *Drosera rotundifolia* | 1 | 52.9 |
| *Eriophorum virginicum* | 2 | 26.5 |
| *Rhynchospora alba* | 3 | 14.7 |

*jus, S. recurvum,* and *Warnstorfia fluitans,* had an increased prevalence (Vitt and Bayley 1984). At Little Dollar Lake, this same suite of species was observed on the *Sphagnum* lawns.

The *Sphagnum* lawn was also the only habitat in the peatland where the orchids *Calopogon tuberosus* (L.) B.S.P. and *Pogonia ophioglossoides* (L.) Ker Gawler grew. *Calopogon tuberosus* grew in all *Sphagnum* lawn habitats, whereas *P. ophioglossoides* was limited to the lawn of the northwestern mat. Both of these orchids are abundant in northern Michigan peatlands, but were surprisingly scarce at Little Dollar Lake.

The *Sphagnum magellanicum–Sarracenia purpurea* PHS on the northwestern floating mat was pock-marked by large, irregular holes in the mat that often were colonized by two submersed species, *Potamogeton confervoides* Reichb. and *Utricularia geminiscapa* Benj. Presumably, these holes had been accentuated and possibly maintained by beaver activity. The edges of these holes were fringed with exposed peat and were the only sites for *Ly-*

*copodiella inundata* (L.) Holub [*Lycopodium inundatum* L.] and *Drosera intermedia* Hayne. Other species that grew on this exposed peat included *D. rotundifolia* L., *Eriocaulon aquaticum* (Hill) Druce [*E. septangulare* With.], *Menyanthes trifoliata* L., *Rhynchospora alba* (L.) Vahl., and the liverwort *Cladopodiella fluitans.*

The *Sphagnum magellanicum–Sarracenia purpurea* PHS closely resembled a similar community at Mud Pond Bog (Moultonborough, NH). Both lawn communities were saturated, spongy habitats extensively colonized by insectivorous plants (*Sarracenia purpurea, Drosera intermedia,* and *D. rotundifolia*), as well as stunted ericaceous species, especially *Chamaedaphne calyculata* (C. E. Hellquist, ms. in prep.). These lawn habitats at Moultonborough were also the preferred habitats of *Pogonia ophioglossoides* and *Calopogon tuberosus* (C. E. Hellquist, ms. in prep.) and corresponded well to the *Sphagnum* lawn concept of Crum (1988). The *Vaccinium oxycoccos–Rhynchospora alba* subtype of Mud Pond Bog (Hillsborough, NH), characterized by dwarfed ericaceous shrubs as well as *D. rotundifolia* and *S. purpurea* (Dunlop 1987), also was similar to the species assemblage at Little Dollar Lake. In Ohio, similar species inventories have been recorded in *Sphagnum* lawn communities (Andreas and Bryan 1990).

### 3. *Chamaedaphne calyculata–Triadenum fraseri* Cover Type

The *Chamaedaphne calyculata–Triadenum fraseri* CT was composed of two phases that exhibited possible terrestrialization patterns in two distinct areas of the peatland. One phase of this cover type was associated with terrestrialization at the lake margin (the *Sphagnum papillosum* PHS) and the other phase was associated with terrestrialization of the stream channel (the *S. majus* PHS; Figure 3). This cover type has been renamed and is identical to the *C. calyculata–Carex lasiocarpa* CT first described by Hellquist (1996) at Little Dollar Lake.

This cover type represents a hybrid association colonized by species common to both the *Chamaedaphne calyculata* CT and the *Calamagrostis canadensis* CT (Table 8). Few species were restricted to this cover type, thus it is defined more by the absence of certain species than those present in its marsh-like physiognomy. Despite its low cover value, *Triadenum fraseri* (Spach) Gleason was a frequent component of this cover type and was

Table 8. Mean percent cover and percent frequency of dominant and associated species in the *Chamaedaphne calyculata–Triadenum fraseri* cover type (32 quadrats). Species having less than 10% frequency are not included in the table. *TWINSPAN indicator species. *Sphagnum cuspidatum* also was designated as an indicator species, but does not appear in the table.

| | Mean % Cover | % Frequency |
|---|---|---|
| BRYOPHYTES | | |
| *Sphagnum recurvum** | 45 | 50.0 |
| *Sphagnum majus** | 60 | 34.4 |
| *Sphagnum papillosum** | 44 | 28.1 |
| *Sphagnum magellanicum* | 13 | 18.8 |
| VASCULAR PLANTS | | |
| *Chamaedaphne calyculata* | 44 | 93.8 |
| *Triadenum fraseri* | 3 | 59.4 |
| *Carex lasiocarpa* | 31 | 56.3 |
| *Carex oligosperma** | 15 | 34.4 |
| *Vaccinium macrocarpon* | 26 | 34.4 |
| *Carex canescens** | 25 | 25.0 |
| *Calamagrostis canadensis* | 24 | 21.9 |
| *Drosera rotundifolia* | 1 | 21.9 |
| *Carex utriculata* | 4 | 18.8 |
| *Glyceria canadensis* | 2 | 18.8 |
| *Acer rubrum* | <1 | 18.8 |
| *Potentilla palustris* | 3 | 12.5 |
| *Sarracenia purpurea** | 4 | 12.5 |

readily apparent with its distinct growth form and reddish-hued foliage (Table 8). *Triadenum fraseri* was commonly seen in more minerotrophic microhabitats along the lakeshore, stream channel, and in the lagg.

Although prominent in the *Calamagrostis canadensis* CT, *Carex lasiocarpa* was also conspicuous in this cover type with a cover of 31% and 56.3% frequency. In the stream channel, the distinct physiognomy of the *C. lasiocarpa* community traced the course of the stream channel from its origin in the muck pools of the southern mat extension, through the ericaceous scrub of the southern mat to the open water of the lake (Figures 1 and 3).

*Carex lasiocarpa* is indicative of more minerotrophic conditions (e.g., Crum 1988; Jeglum 1971; Schwintzer 1978; Vitt and Bayley 1984; Vitt and Slack 1975). With its prolific interlaced rhizome sytems, *C. lasiocarpa* is one of the most important lake-fill species that can initiate the process of terrestrialization along shorelines (Gates 1942). In northern Michigan, *C. lasiocarpa* is

Table 9. Mean percent cover and percent frequency of dominant and associated species in the *Sphagnum majus* phase of the *Chamaedaphne calyculata–Triadenum fraseri* cover type (22 quadrats). Species having less than 10% frequency are not included in the table. *TWINSPAN indicator species.

| | Mean % Cover | % Frequency |
|---|---|---|
| BRYOPHYTES | | |
| *Sphagnum recurvum** | 51 | 63.6 |
| *Sphagnum majus** | 64 | 45.5 |
| VASCULAR PLANTS | | |
| *Chamaedaphne calyculata* | 43 | 95.5 |
| *Carex oligosperma** | 15 | 45.5 |
| *Calamagrostis canadensis** | 28 | 27.3 |
| *Vaccinium macrocarpon** | 40 | 27.3 |
| *Carex utriculata* | 5 | 22.7 |
| *Glyceria canadensis* | 3 | 22.7 |
| *Acer rubrum* | <1 | 22.7 |
| *Potentilla palustris* | 3 | 18.2 |
| *Drosera rotundifolia* | <1 | 18.2 |
| *Carex canescens* | 8 | 13.6 |

the primary mat-forming species along more alkaline lake margins with circumneutral pH values (Crum 1988; Vitt and Slack 1975). A circumneutral sedge mat dominated by *C. lasiocarpa* has also been noted in southern Michigan (Crow 1969). At Red Lake peatland in Minnesota, *C. lasiocarpa* was the most abundant vascular plant in open rich fens (Wheeler et al. 1983). Similarly, in north-central New Hampshire, the presence of *C. lasiocarpa* along lake edges and in wet habitats with a fen-like flora has also been noted (Fahey and Crow 1995; C. E. Hellquist, ms. in prep.).

### 3A. *Sphagnum majus* Phase

The *Sphagnum majus* PHS was a relatively minerotrophic phase that was contained within the stream channel that originated in the southeastern lagg of the southern mat extension, and eventually reached the open water of Little Dollar Lake. The *S. majus* PHS also comprised the narrow eastern and western mats (Figure 3). Both of these mats bordered steep upland slopes and were dominated by *S. majus* and *S. recurvum* (Table 9). Conspicuous vascular plants on these mats included *Carex canescens, C. lasiocarpa, Calla palustris* L., *Chamaedaphne calyculata, Vaccinium macrocarpon* Aiton, and *Triadenum fraseri*. The relative minerotrophy of this vegetation phase was strongly suggested by the presence of *S. subsecundum.* This minerotrophic species is often found in open, wet lagg habitats and sedge mats (Andrus 1980; Crum 1983, 1988), and has been shown to grow in moderately acidic habitats (ca. pH 4.5–6.0; Gorham and Janssens 1992b). This phase was the only area in the peatland where *S. subsecundum* grew in abundance (Hellquist and Crow 1997).

### 3B. *Sphagnum papillosum* Phase

The *Sphagnum papillosum* PHS occurred along the majority of the lake margin. This community was distinguished by a narrow swath (~1.0 m) of *Chamaedaphne calyculata* and *Kalmia polifolia* intermingled with *Vaccinium macrocarpon* and *Triadenum fraseri* that extended into the open water of the lake. Immediately behind this band of *C. calyculata* was a wet trough with some standing water, colonized primarily by *S. papillosum, Carex canescens* L., *C. limosa* L., and *Rhynchospora alba.* Although sampled infrequently, *C. limosa* was a major component of this phase. Other species frequent in this trough included *Cladopodiella fluitans, Sphagnum cuspidatum, S. recurvum, Carex lasiocarpa,* and *Sarracenia purpurea* (Table 10).

The *Sphagnum papillosum* PHS of Little Dollar Lake closely resembled an "acid lake edge" community (Crum 1988; Vitt and Slack 1975) that was also observed at Heath Pond Bog, New Hampshire (Fahey 1993). The acid lake vegetation sequence is characterized by the lack of vascular macrophytes in the lake itself, the presence of *Chamaedaphne calyculata* growing out into open water, *Sphagnum* as a pioneer among *C. calyculata,* frequently a "sparse *Carex* fringe" along the lake, and a narrow *Sphagnum* lawn that quickly merges into a grounded mat (Crum 1988).

Vitt and Slack (1975) defined the "acid lake edge" community by the presence of a *Sphagnum cuspidatum–Sphagnum papillosum–Carex limosa–Carex paupercula* association and a pH range of 5.0–7.0. At Little Dollar Lake, *S. papillosum,* and to a lesser extent *S. cuspidatum,* were the predominant semi-aquatic *Sphagnum* species pioneering the lake margin. *Sphagnum papillosum* frequently becomes more prominent in less saturated microhabitats (Vitt and Slack 1975), although along the lake margin at Little Dollar Lake (mean pH = 4.5, n = 40) *S. papillosum* grew both emergent above the water level, and partially submerged

Table 10. Mean percent cover and percent frequency of dominant and associated species in the *Sphagnum papillosum* phase of the *Chamaedaphne calyculata–Triadenum fraseri* cover type (10 quadrats). Species having less than 20% frequency are not included in the table. *TWINSPAN indicator species.

| | Mean % Cover | % Frequency |
|---|---|---|
| BRYOPHYTES | | |
| *Sphagnum papillosum* | 49 | 80.0 |
| *Sphagnum magellanicum* | 9 | 40.0 |
| *Sphagnum cuspidatum* | 41 | 40.0 |
| *Sphagnum recurvum* | 5 | 20.0 |
| *Sphagnum capillifolium* | 10 | 20.0 |
| VASCULAR PLANTS | | |
| *Chamaedaphne calyculata* | 47 | 90.0 |
| *Triadenum fraseri* | 4 | 80.0 |
| *Carex canescens* | 36 | 50.0 |
| *Vaccinium macrocarpon* | 10 | 50.0 |
| *Carex lasiocarpa** | 22 | 40.0 |
| *Sarracenia purpurea* | 4 | 40.0 |
| *Drosera rotundifolia* | 2 | 30.0 |
| *Eriocaulon aquaticum* | 3 | 30.0 |
| *Kalmia polifolia* | 3 | 30.0 |
| *Vaccinium oxycoccos* | 1 | 30.0 |
| *Rhynchospora alba* | <1 | 20.0 |
| *Scheuchzeria palustris* | 5 | 20.0 |
| *Utricularia geminiscapa* | <1 | 20.0 |

among *Chamaedaphne calyculata* branches in the lake (Hellquist 1996).

In northern Michigan, *Sphagnum papillosum* is known to inhabit wetter, more mineral rich habitats on mats or lake margins influenced by water movement (Crum 1983, 1988). In Ontario, *S. papillosum* is also associated with lake edge vegetation sequences (Vitt and Bayley 1984). The liverwort *Cladopodiella fluitans* also seems to indicate the acid nature of the lake margin community based on its preferred pH range of 3.7 to 5.0 (Gorham and Janssens 1992b). In Maine, sedge-moss lawn communities characterized by *S. papillosum, S. magellanicum, Carex limosa, Rhynchospora alba,* and *Scheuchzeria palustris* were found in "very acidic" to "moderately acidic" fens (Anderson and Davis 1997).

Vitt and Slack (1975) cite *Carex limosa* as being essentially restricted to this zone. At Little Dollar Lake, *C. limosa* was primarily found along the lake margin with the exception of a few scattered localities in wet areas of the *Calamagrostis canadensis* CT. Of the four species described as characteristic of this community by Vitt and Slack (1975), only *Carex paupercula* Michx. was absent at Little Dollar Lake.

### 4. *Potamogeton confervoides–Utricularia geminiscapa* Cover Type

The depauperate aquatic flora of Little Dollar Lake reflected the acidity of the lake water. The aquatic flora consisted of three submersed species (*Isoëtes echinospora* Durieu, *Utricularia geminiscapa,* and *Potamogeton confervoides*) and two floating species (*Nuphar variegata* Durand and *Nymphaea odorata* Aiton). Two submersed and/or emergent species, *Eriocaulon aquaticum* and *Hypericum boreale* (Britton) E. Bickn. forma *callitrichoides* Fassett, were also present in or along the lake (Hellquist 1996; Hellquist and Crow 1997).

*Potamogeton confervoides* and *Utricularia geminiscapa* were concentrated along the periphery of the floating mat, among the submerged rhizomes and roots of ericaceous shrubs growing into the open water of the lake. While *P. confervoides* was especially abundant and fruited copiously in the summer of 1994, it seemed less abundant in 1995, and was not fruiting as prolifically as in 1994. In 1996 the population continued to recede, with the majority of the population scattered along the lake margin of the eastern and southern mats. Previously, it had been found around the entire circumference of the lake.

In Michigan, *Potamogeton confervoides* occurs locally in lakes and acid bogs (Voss 1972) and is listed as a state of Michigan Threatened Species (Anonymous 1994; Beaman et al. 1985), although its status as Threatened may be due to under-collection rather than to actual rarity. In New England, *P. confervoides* is associated with soft waters, including high elevation ponds and lakes (Hellquist 1980). It is characteristic of extremely acidic waters with low alkalinity values (maximum alkalinity value 8.5 mg/l $CaCO_3$) and is the only pondweed found in *Sphagnum* bog ponds (Hellquist 1980).

*Utricularia geminiscapa* was also found submersed along the edge of the floating mat. In New England, *U. geminiscapa* is associated with bog ponds and acidic to moderately alkaline waters with a pH of 3.5–8.6 and alkalinity of 5.4–69.5 mg/l $CaCO_3$

(Crow and Hellquist 1985). Like *Potamogeton confervoides,* the abundance of *U. geminiscapa* was noticably lower in 1996 than in the two previous years.

*Isoëtes echinospora* grew submersed in the sandy sediments on the bottom of Little Dollar Lake. Individuals tended to grow widely scattered and were most conspicuous in shallow water off the eastern mat. In 1996, *Hypericum boreale* forma *callitrichoides,* an aquatic to partially emergent growth form, was thriving in the water along the edge of the eastern mat.

**Evidence of terrestrialization and small-scale paludification processes at Little Dollar Lake.** In an analysis of the pollen and sediment stratigraphy of Little Dollar Lake, Futyma (1982) stated that since the formation of the peatland approximately 3500 years before present, at least fifty percent of the surface area of Little Dollar Lake had been covered by peatland vegetation. At the time of this study, evidence of these terrestrialization patterns was visible at Little Dollar Lake in the former stream channel as well as in the muck pool area of the southern mat extension.

Apparent botanical evidence of terrestrialization was observed in the muck pools of the *Sphagnum cuspidatum–Dulichium arundinaceum* PHS of the *Calamagrostis canadensis* CT, and in the various areas of the *S. majus* and *S. papillosum* phases of the *Chamaedaphne calyculata–Triadenum fraseri* CT (Hellquist 1996). In these areas there was evidence from relict aquatic vegetation, as well as from aerial photography, that previously aquatic habitats were being colonized by emergent wetland vegetation (Hellquist 1996).

At Little Dollar Lake peatland, apparent on-going terrestrialization was most conspicuous at the muck pools in the southeastern lagg of the southern mat extension. These muck pools experienced conditions that vacillated between exposure and submergence. Along the edges of these mucky areas *Chamaedaphne calyculata, Carex lasiocarpa, Dulichium arundinaceum,* and *Glyceria canadensis,* as well as other emergent vascular species, were well established and were apparently encroaching into the open areas of peaty muck.

In 1994 and 1995, the muck pools contained stranded aquatic vascular plant species that were directly subjected to the fluctuating water levels of the peatland. One of the stranded aquatic species was *Potamogeton oakesianus* Robbins, which grew stunted and infertile with "floating" leaves lying on the surface of the mucky peat. Another stranded aquatic species, *Sparganium minimum* (Hartman) Fries, was found fruiting abundantly along the edges of the muck pools. *Utricularia intermedia* Hayne also grew in the peaty muck. In 1995, *U. intermedia* was extremely scarce with less than ten individuals located. However, when the muck pools were flooded in 1996, *U. intermedia* was frequent, with many lush, thriving individuals growing among the emergent vegetation.

There was also evidence of terrestrialization in the stream channel that wound through the southern mat and southern mat extension. The intermittently aquatic stream channel was colonized by a tenuous, loose network of *Carex lasiocarpa* that readily sank and quaked extensively when walked upon. This channel was also home to approximately 25 emergent clusters of stranded *Nuphar variegata* that were surrounded entirely by *C. lasiocarpa* and scattered individuals of *Potentilla palustris* in an approximately 3.0 m × 3.0 m area (Hellquist 1996). In a 1978 infrared aerial photograph, this stream channel was visible as open water whereas 1995 aerial photos and concurrent ground surveys clearly showed that, although still visible, the channel had become entirely covered by a quaking mat of vegetation dominated by *C. lasiocarpa* (see Hellquist 1996 and Hellquist and Crow 1997 for photographs).

Water levels in 1994 and 1995 were relatively low, but in 1996 the stream channel and muck pool areas became partially submerged by high water levels. In most areas, the *Sphagnum majus* PHS was covered by water with a minimum depth of ca. 20 cm. Presumably during high water years, terrestrialization by emergent sedges and other wetland taxa such as *Potentilla palustris* probably does not progress as rapidly as in drier years. Therefore, if the peatland experiences more dry years than wet years, expansion of the sedge-dominated mat would continue, and peat deposition and plant colonization would further promote terrestrialization. This process could occur relatively rapidly in an area as confined as the stream channel.

A similar rapid terrestrialization process has occurred at Weber Lake Bog in Cheboygan County, Michigan. A small pool of open water fringed by *Carex lasiocarpa* was mapped by University of Michigan Biological Station ecology classes in 1967 (Vitt and Slack 1975). When examined by Vitt and Slack in the mid-1970s neither the open water nor *C. lasiocarpa* was present. The pool was replaced by an open mat community with stranded clumps of *Dulichium arundinaceum.* During the summer of 1995, the area that had once been open water was still apparent, and contained stranded individuals of *Nuphar variegata,* as well as a few isolated individuals of *C. limosa. Carex lasiocarpa* has remained absent at Weber Lake Bog (E. G. Voss and C. E. Hellquist, pers. obs. 1995).

In some lagg areas of the *Iris versicolor–Lycopus uniflorus* PHS at Little Dollar Lake, small-scale paludification was observed where *Sphagnum* spp. were growing onto upland slopes. The process of paludification often is associated with rising water levels, especially in shallow, flat basins (Crum 1988). In some basin peatlands in northern Michigan, paludification is initiated by the compression of the lowermost peat layers. These compacted layers become so tightly condensed that they act as a sealant that prevents water from percolating out of the basin. Thus, any water entering the basin is retained by the more porous upper peat layers (Futyma 1982). This sequence is believed to have resulted in paludification at other Michigan peatlands, including Tahquamenon Bog and the Trout Lake peatlands in Chippewa County (Futyma 1982) and Lake Sixteen peatland in Cheboygan County (Futyma and Miller 1986). At Little Dollar Lake, the gradual creep of *Sphagnum* onto upland soils in some areas can probably be attributed to pooling of water trapped in the lagg.

Based on pollen and stratigraphic analysis from Futyma (1982), as well as field and photographic evidence described by Hellquist (1996) and Hellquist and Crow (1997) there seems to be satisfactory botanical evidence illustrating terrestrialization and paludification processes at Little Dollar Lake peatland. The patterns observed follow the "bog climax model" of peatland succession proposed by Klinger (1996), where areas of water are colonized by extensive, but irregular growth of vegetation while paludification proceeds as peat is deposited over upland soils along the margin of the bog basin. At Little Dollar Lake the areas along the lakeshore, stream channel, and muck pools with stranded aquatic taxa seem to be indicative of terrestrialization processes whereas paludification is less easily discerned, but still present in some lagg areas.

**Little Dollar Lake peatland classification.** The majority of northern Michigan peatlands exist in glacial topography and remain under the influence of local hydrology. Despite the fact that most of these peatlands are dominated by *Sphagnum,* they are best classified as fens (Vitt et al. 1975). Little Dollar Lake corresponds well to the delineation of a northern Michigan poor fen or "bog" (i.e. a more acid, oligotrophic peatland) as defined by Schwintzer (1981). Schwintzer (1981) states that these peatlands are weakly minerotrophic with low pH values (3.8–4.3) and low concentrations of calcium cations (1.2–3.7 mg/L). These poor fen complexes have a prominent *Sphagnum* cover, low vascular species richness, well developed open areas dominated by ericaceous shrubs, and reduced tree cover (Schwintzer 1981).

This study and its companion studies (Hellquist 1996; Hellquist and Crow 1997) have documented the flora and described the vegetation patterns within Little Dollar Lake peatland. This analysis, used in conjunction with the postglacial history of the Little Dollar Lake basin (Futyma 1982), has laid a foundation for subsequent studies that may further elucidate the dynamic processes (e.g., hydrology, nutrient regimes, interspecific plant interactions, plant-herbivore interactions, successional patterns) that influence the abundance and distribution of peatland vegetation at Little Dollar Lake.

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RHODORA, Vol. 101, No. 905, pp. 87–91, 1999

## NOTE

# MORE MOLECULAR EVIDENCE FOR INTERSPECIFIC RELATIONSHIPS IN *LIQUIDAMBAR* (HAMAMELIDACEAE)

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There are four species of *Liquidambar* L. (Altingioideae, Hamamelidaceae). *Liquidambar orientalis* Miller occurs in western Asia and *L. styraciflua* L. in Northern and Central America, while *L. acalycina* Chang and *L. formosana* Hance are found in southeastern Asia (Bogle 1986). A phylogenetic analysis has recently been conducted based on DNA sequences of the plastid gene *mat*K (Li et al. 1997a). Li et al. found that the western Asian species *L. orientalis* is most closely related to the New World species *L. styraciflua*. This result is consistent with an earlier allozyme study (Hoey and Parks 1991). The finding is significant because it suggests a possible phytogeographical connection between the western Eurasian continent and the New World.

The close relationship of *Liquidambar styraciflua* and *L. orientalis* is moderately well supported by bootstrap values in the *mat*K analysis and no homoplasy was found. However, there are only seven phylogenetically informative characters in the data set. Therefore, it is desirable to gather more evidence to test this phylogenetic hypothesis. In this note, we report recent progress.

Three more regions of DNA have been sequenced, including the ITS (Internal Transcribed Spacer) region of nuclear ribosomal DNA (Baldwin et al. 1995), the intron of chloroplast gene *trn*L (Taberlet et al. 1991), and the exon 9-exon 12 region of the *GBSS* (Granule-Bound Starch Synthase) gene (Dai et al. 1996; Mason and Kellogg, unpubl. data).

DNA extraction, sequencing reactions, and PCR (Polymerase Chain Reaction) amplification for ITS were conducted as described in Li et al. (1997b, 1997c). PCR amplification of the *trn*L intron was carried out using primers c and d of Taberlet et al. (1991) with a thermocycler program of 30 cycles of 94°C for 35 sec., 55°C for 30 sec., and 72°C for 95 sec. The final cycle was followed by a seven minute extension at 72°C. PCR amplification of the *GBSS* gene was conducted using primers *GBSS*F2 (5′TGGCATGGATACCCAAGAGT3′) and *GBSS*R2 (5′CCTTCTTTCACAGTGTCAAC3′). We have successfully amplified a fragment of about 800 base pairs for several flowering plant taxa, including *Hamamelis* (Hamamelidaceae), *Stewartia* (Theaceae), and *Viburnum* (Adoxaceae). The thermocycler program consisted of a 60 sec. hotstart at 96°C and 40 three-temperature cycles, followed by a 15 minute extension at 72°C. Each cycle had denature and extension temperatures of 96°C for 60 sec. and 72°C for 90 sec., respectively. The annealing temperatures were 56°C, 54°C, and 52°C for the first two cycles, the second two, and the remaining 36 cycles, respectively. The annealing time was 60 sec. for all cycles. Sequencing reactions were carried out using Amersham cycle sequencing kit (Amersham Life Science Inc., Arlington Heights, IL) and following the manufacturer's instructions. Sequences were determined with an ABI 377 automated sequencer (Applied Biosystems, Inc. Foster City, CA). We obtained 348 base pairs from the ITS region (partial 5.8S plus ITS-2), 524 sites from the *trn*L intron, and 776 base pairs from the *GBSS* gene.

The parsimony analyses were conducted using the exhaustive tree search option of PAUP 3.1.1 (Swofford 1993). Trees were rooted using the same outgroup, *Mytilaria laosensis* Lecompte, as in the previous study (Li et al. 1997a), except that *Exbucklandia* R. W. Br., which is closely related to *Mytilaria* (Li et al. unpubl.), was used for the *GBSS* data set because we were unable to amplify the *GBSS* gene for *Mytilaria* due to its genomic DNA deterioration. Decay analysis (Donoghue et al. 1992) and 1000 bootstrap replicates (Felsenstein 1985) were carried out to indicate the relative support for the clades. Characters were unordered and unweighted, and gaps were treated as missing data.

The ITS data contained 82 variable sites, 15 of which were phylogenetically informative. The interspecific divergences between *Liquidambar* species ranged from 0.9–6.6%. A single most parsimonious tree was generated based on the ITS data set with a consistency index of 0.99. The tree was comprised of two clades, one of which contained *L. acalycina* and *L. formosana* and was supported by a bootstrap percentage of 100% and a decay index of nine steps. The other clade was composed of *L. orientalis* and *L. styraciflua* and was not strongly supported, with bootstrap and decay values of 69% and one step, respectively.

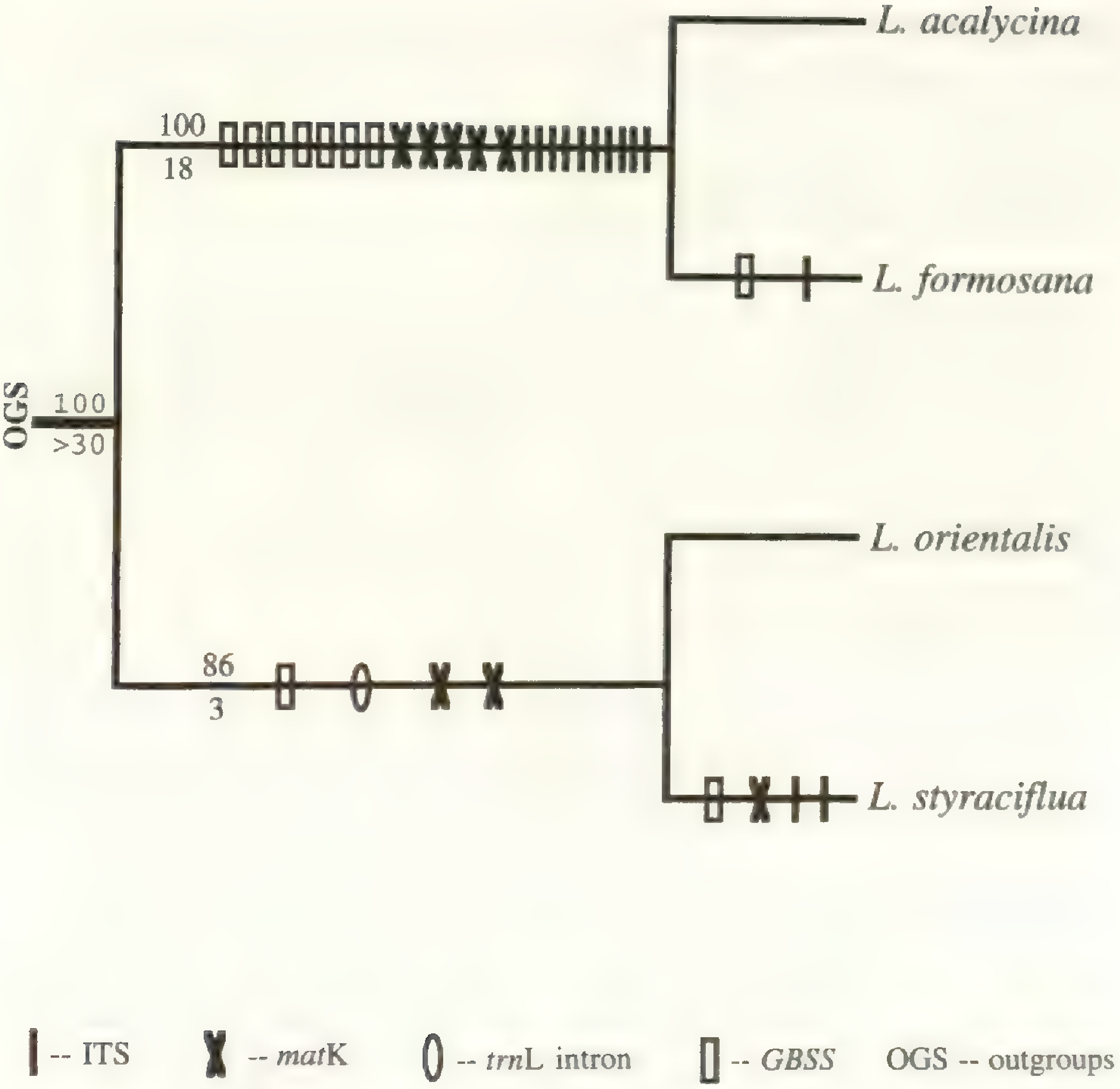

Figure 1. The single most parsimonious tree of 535 steps of *Liquidambar* based on sequences of ITS, *mat*K, *GBSS*, and *trn*L intron. CI = 0.98. Numbers above and below the branches are bootstrap percentages and decay index values, respectively. Symbols represent unambiguous, potentially informative changes of each data set along the branches.

The *trn*L intron data set had 21 variable sites, two of which were phylogenetically informative. The sequence divergences between *Liquidambar* species were from 0–0.8%. *Liquidambar acalycina* and *L. formosana* had identical *trn*L intron sequences. The parsimony analysis generated two equally short trees, one of which showed the tree topology produced by the ITS data, while the other tree did not resolve the relationships of *L. formosana, L. acalycina,* and the clade of *L. orientalis* and *L. styraciflua*. The consistency index was 1.0.

There were 105 variable sites in the *GBSS* data set, 15 of which were informative. Parsimony analysis resulted in one single shortest tree of 111 steps, with a consistency index of 0.96. In the phylogenetic tree, eight and seven informative sites supported the clade of *Liquidambar orientalis–L. styraciflua* and *L. acalycina–L. formosana,* respectively. Bootstrap values for the two clades were 78% and 82%, respectively.

The four data sets were congruent, including *mat*K, ITS, *trn*L intron, and *GBSS,* and the combination of them created a data set of 3164 characters. The parsimony analysis, using both *Exbucklandia* and *Mytilaria* as outgroups with *Mytilaria GBSS* sequences coded as missing data, produced a single most parsimonious tree with a consistency index of 0.98. The phylogenetic tree showed the same species relationships as described in Li et al. (1997a). Both bootstrap percentages and decay values were high, 100% and 18 steps for the *L. acalycina–L. formosana* clade, and 86% and three steps for the clade of *L. orientalis* and *L. styraciflua.* Figure 1 shows the number of unambiguous changes from each of the four data sets that support the two clades.

This follow-up study strongly substantiates the previous hypothesis that the western Asian species *Liquidambar orientalis* is more closely related to the New World species *L. styraciflua* than to the southeast Asian species. Additionally, we conclude that sequences of the *GBSS* gene, especially the introns, provide another informative nuclear marker (besides nrDNA ITS) in resolving phylogenetic relationships among closely related species.

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## BOOK REVIEW

*The Savage Garden: Cultivating Carnivorous Plants* by Peter D'Amato. 1998. xxii + 314 pp. more than 200 photographs and illustrations, most in color. ISBN 0-89815-915-6 $19.95 (paperback). Ten Speed Press, Berkeley, CA.

Carnivorous plants, a group of about 500 species and numerous cultivars, have captivated botanists, horticulturalists, and students of all ages since Darwin (1875) wrote one of the earliest books on the group. The more easily grown species and those locally abundant in boggy areas have been widely employed by teachers to stimulate interest in young students in plant biology and ecology. Unfortunately, until recently, little information has been available in book form in public and college libraries for teachers and students who want to know more about growing these plants. In recent years, three books with a worldwide scope have been published and widely distributed: Pietropaolo and Pietropaolo (1986), Lecoufle (1989, in translation), and Cheers (1992). These three works cover some of the same ground as the earlier and excellent books by Slack (1980, 1988) which are difficult to obtain.

Peter D'Amato's book surpasses these earlier works in the sheer volume of cultivation information and lore provided for individual species and cultivars. It is based on Peter's many years of experience with growing these plants; of selling them through his greenhouse, mail order and Internet nursery, California Carnivores; and of making numerous presentations at schools, hobbyist meetings, and on television. His goal, as he described it during a talk at the first meeting of the International Carnivorous Plant Society in Atlanta in 1997, was to popularize the plants and show how they can be grown in a wide variety of ways indoors and out. The range of creative, and sometimes whimsical, ways to grow these plants, well illustrated and described in the book, is its strongest feature. Since the book covers species worldwide, it also provides a starting point for exploring plant diversity and plant geography. The amazing radiation of *Drosera* species in Australia, and the narrowly restricted endemic genera *Darlingtonia, Heliamphora,* and *Cephalotus* which use trapping mechanisms similar to *Sarracenia* and *Nepenthes* are good examples.

A few minor faults should be noted. Many of the color photographs are small, but this allows for more text to flow around the figures creating a tighter integration of the two. On the other hand, this design foregoes including any large *in situ* shots such as those in Schnell's (1976) *Carnivorous Plants of the United States and Canada* or Clarke's (1997) truly stunning book on the *Nepenthes* of Borneo. As noted in the review published in the September (1998) issue of the *Carnivorous Plant Newsletter*, there are some spelling errors and some of the cultivars listed are not well documented in the literature. Readers interested in an overview of the unique physiological and ultrastructural features of carnivorous plants may wish to supplement this book with the earlier work by Juniper et al. (1989). Some of the guidelines presented for growing individual species may be less effective outside the northern California climate where the author lives. Apparently, no hardcover edition is available.

Overall, the well named *Savage Garden* is a bargain for the wealth of information it contains. As a CP enthusiast, I use it often. It may well achieve "bible" status for growers of these plants, especially as tissue culture (described in the first Appendix by expert Rob Gagliardo) makes more species available to the general public. I would recommend this book for all libraries, and to botanists and horticulturalists as a one-book gateway to knowing more about these fascinating plants.

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# NEBC MEETING NEWS

**October 1998.** Dr. Lisa A. Standley, the Club's Vice President, spoke on the topic "Beyond the Brooks Range—Flora and Fauna of the Arctic National Wildlife Refuge." Among Dr. Standley's many activities, we learned, is participating in Sierra Club outings. Twice in recent years, she has enjoyed ten-day backpacking trips to the Arctic National Wildlife Refuge in northeastern Alaska. Both trips were in mid-June, and started with a flight into Fairbanks and transfer to a smaller plane that flew through passes in the Brooks Range to the Romanzof Mountains and the coastal plain of the Beaufort Sea, a couple of hundred miles north of the Arctic Circle. The area hiked was between two rivers, the Jago and the Aichilik, which flow northward from the mountains, crossing the coastal plain to the sea. The Refuge is contiguous with Indian lands and National Parks, which add to the wilderness landscape. It is home to the caribou's Porcupine Herd calving grounds and their migration routes to the mountains. Fortunately for us, Lisa was armed with a good camera and the ability to use it well. We were treated to excellent images of the region's plant life, interspersed with those of the often present and possibly curious caribou. Also, landscape shots illustrated some of the Refuge's varied habitats and unadulterated beauty. The hiking area ranged in elevation from near sea-level to around 5000 ft. Most of the landscape is devoid of tall trees, although some of the narrower valleys supported white and black spruce in sheltered areas. Low willows were the more typical woody vegetation. The narrow valleys generally run east-west while larger river valleys run north-south. Precipitation is surprisingly low there, with only about 10 inches per year, Standley said. The few glaciers seen while crossing the Brooks Range were relatively small and not growing, evidently remnants of earlier times with higher rates of precipitation.

The slide images gave a good sampling of the dominant plant families in the Refuge and the Arctic region, in general. The Cyperaceae, a family Standley knows especially well because of her research on the genus *Carex,* is one of them. Sedges were well represented and tipsy tussocks of cottongrass were frequently underfoot. More frustrating for Lisa than the tipsy tussocks, perhaps, was that nearly all the sedges present in June were flowering rather than fruiting, making identification very challenging. Another family well represented was the Salicaceae. A favorite for Standley was *Salix minima* which stood less than an inch tall with catkins of reddish flowers. The Saxifrage family was represented by several species of *Saxifraga* including *S. oppositifolia,* a circumboreal species present in New England, and the very unusual *S. eschscholtzii* with its tiny cushion-like rosettes of succulent leaves only 2 mm across. Jumping to the Rose family, we saw *Potentilla hypartica* (or *P. nana,* in some books), a close relative of New England's federally endangered *P. robbinsiana.* Also representing the Rosaceae were both species of *Dryas.* The hikers liked seeing *Dryas,* since it meant they would be walking on gravel substrate and not wobbly tussocks. Ericads were also represented in the tundra by white flowering *Cassiope* [or *Harrimanella* in some references], pink flowered *Rhododendron lapponicum* described by Standley as weedy everywhere, and *Loiseleuria* seen at around 5000 ft. elevation.

Also illustrated by Standley were: a *Douglasia* species (Primulaceae) which is endemic to Alaska and the Yukon; a *Hedysarum* (Fabaceae) which has aromatic, edible roots eaten by grizzly bears; yellow poppies, which trap heat and attract flies in cup-like flowers that tilt toward the sun, which in June's solstice sky shines for 24 hours per day; nitrophilous, orange-colored lichens growing on rocks where birds perch; caribou trails made in the tundra in the 1940s; caribou skeletons used for drying wet socks; musk-oxen simulating "fringed sofas" swaying in the breeze; aerial views of river meanders revealing a hundred or more years of geomorphology; vertical Jurassic formations with marine fossils; cliffs with gyrfalcon nest sites; sloping bogs at 4000–5000 ft.; and a grizzly sow with cub.

Standley recommended Pielou's *Arctic Naturalist* and *Birds of Alaska.*

**November 1998.** Dr. Bruce Lindwall, a recent graduate of the University of Massachusetts, spoke on the topic "The Effects of Habitat Fragmentation on Plants." Dr. Lindwall first thanked the New England Botanical Club for awarding him (in 1996) a Graduate Student Research Award to support his dissertation research. He then launched into a fascinating presentation of his dissertation research findings about genetic diversity in populations of three alpine tundra species, comparing fragmented populations from nine peaks in the Adirondack Mountains of New York with nine sample sites within a continuous, unfragmented habitat of the Presidential Range in the White Mountains of New Hampshire. Previous studies on the effects of fragmentation on loss of genetic diversity, he said, have involved habitats with a relatively recent history of fragmentation (i.e., less than a few hundred years) and only one taxon. He thought, by examining high peak populations presumably separated for thousands of years, that the effects of time on genetic drift and genetic diversity might be more apparent. By examining three species, he hoped to reduce the possibility of any erroneous conclusions made by assuming that what is true for one is true for all. Lindwall identified the three key questions he wanted to answer in the study as: 1) Do fragmented plant populations in the Adirondack peaks have less diversity than the continuous population in the White Mountains? 2) Is there more gene flow in the Presidential Range than among the fragmented populations in the Adirondacks? 3) What effect does greater habitat area have on diversity in the White Mountains versus the smaller area for each of the isolated Adirondack sites?

A fortuitous coincidence of Lindwall's site design, he added, was that the overall land area and distances between sites for the two study areas were approximately the same. To quantify the relative abundance and frequency of each species, 6000 plots, each one $m^2$, were examined. The genetic diversity was assessed using allozyme analysis. The three species studied were *Minuartia groenlandica,* which appears to be exploiting disturbed trail-edge habitat, *Carex bigelowii,* which forms large patches in the White Mountains, and *Diapensia lapponica,* a monotypic genus found in tundra. Three thousand tissue samples were taken and analyzed during the study.

For each of Lindwall's three questions, the answers were "yes," "no," and "maybe." Did the fragmented Adirondacks have lower genetic diversity? For *Diapensia lapponica,* the answer was a statistically significant "yes," but for *Minuartia groenlandica,* he found higher diversity at all Adirondack peak sites than at the Presidential Range subsites. The results for *Carex bigelowii* were not as easy to interpret. The overall genetic variability was higher in the White Mountains, but because *C. bigelowii* is less abundant in the Adirondacks than the Presidential Range, the sample size was small and only one of four indices was higher, statistically. Thus, we have a "maybe." What about gene flow? Lindwall created dendrograms to illustrate degrees of similarity (or difference) in both genetics and geographic distances among the populations. Comparing Nei's index of genetic identity for each of the three species relative to the Adirondacks and Presidentials, the answers were again mixed. For *C. bigelowii,* there was a close relationship among all sites in New Hampshire but not so among the New York sites. *Minuartia groenlandica,* on the other hand, showed no particular pattern with generally good gene flow across the board. However, the most genetically distant population in the Adirondacks was from the most distantly isolated peak, the Gothics. The story with *D. lapponica* also seemed to relate to distance between sites. In both areas there appeared to be good gene flow with near neighbors, such as among the four McIntyre Ridge peaks in the Adirondacks, but less so when distance was greater between sites. What role does habitat area play? With *C. bigelowii,* there was a clear relationship: bigger places had more variability. Just the opposite was true for *Minuartia*: the smaller sites in the Adirondacks had statistically higher variability than the continuous population in the Presidentials. For *Diapensia,* size appeared to have no effect, and thus we have a "maybe" answer.

There was one general conclusion that fit all three species, Lindwall said in summary: The greatest amount of genetic diversity occurs where each species is the most abundant. He also concluded that we should neither assume that species will behave the same despite similar histories, nor for conservation planning purposes assume that the largest habitat area will support the most diverse population of a given species.

**December 1998.** The program, entitled "Verdant Venues and Ventures: Visible and Verbal Visions" represented the annual event where Club members are invited to make short presentations on their explorations over the year. Keith Williams led off with images from a South America vacation trip with his wife in May. It was the middle of the dry season in Brazil, their first destination, but they still saw lots of water because much of their time was spent on the coast and in the Pantanal, a huge wetland that extends into two other South American countries. Plants featured in the slide images were *Tabebuia alba,* an endangered tree species in Brazil; *Cuphea melvilla,* a prolific shrub along the Pantanal waterways; and *Ludwigia inclinata* and *Cabomba furcata* growing in sloughs and shallows of the Pantanal. He ended with shots from Peru's Inca Trail to Machu Picchu and an image of an *Equisetum* growing from the mortar of stone ruins.

Marsha Salett followed Keith with a brief introduction to her Master's degree project at the University of Massachusetts—Boston which is to create a CD-ROM version of a natural history guide to bogs of southern New England. She showed images of several bogs with public access that she might feature in the guide, as well as a few that lack easy access or boardwalks that she may omit. Her intent is to present explanations and illustrations of bog types and common species such as *Kalmia angustifolia* and *Ledum groenlandicum.* Dichotomous keys and images of plants in flower and fruit will be provided to help with identifications.

Lois Somers then took us back to the tropics with images of a trip with husband Paul to Costa Rica. Being a registered nurse, not a botanist, she used a few wildlife images to illustrate some of the critters botanists need to be on the watch for while probing the greenery. The images included an orange-kneed tarantula seen in the Monteverde cloud forest and an eyelash viper seen at Braulio Carrillo National Park. Aquatic critters to be aware of included caiman seen on the Cano Negro River near the Nicaraguan border and the much larger and fiercer crocodiles of the Palo Verde region.

Joanne Sharpe's slides started in Costa Rica with an image of *Danaea wendlandii,* one of the fern species she studied there for six years. She then took us to Puerto Rico for a look at disturbance studies of ferns in a palm forest before and after Hurricane Georges, and in mangrove swamps, where the 14 ft. tall leather fern, *Acrostichum danaeifolium,* was regenerating following four years of hydrologic disturbance from dike construction. Her last stop was Maine with images from the Coastal Maine Botanical Gardens in Boothbay, where *Nyssa sylvatica* can be found at or near its northern limit.

David Hunt continued the regional theme with images from New York where he has been helping to refine the state's plant community classification, particularly in the Northern Appalachian Ecoregion. His images included riverside ice meadows with *Prunus pumila* and *Andropogon gerardii* and pine-dominated rocky summit communities with either pitch or red pine and associates such as *Vaccinium myrtilloides, Amelanchier bartrami-*

*ana*, and *Oryzopsis pungens*. He then took us underwater at Lake George where he has been doing underwater vegetation sampling at depths up to 40 ft. In shallow bays he found *Potamogeton amplifolius–Vallisneria americana* and *Eriocaulon aquaticum–Elatine americana* to be common community types, whereas sandy deltas had associations of *Lobelia dortmanna* and *Myriophyllum pinnatum*. In deeper waters he found associations of *Najas flexilis, Potamogeton gramineus,* and *P. perfoliatus*. At 30 ft., he found beds of *Isoetes macrospora* and *Potamogeton robbinsii*, and at 40 ft., a dense cover of *Nitella flexilis*. With this success, he's now tackling marine eelgrass environments of Long Island.

The next three presenters came as a team representing the newly formed Botanical Club of Cape Cod and the Islands. Don Schall spoke about the group's search for and likely rediscovery of an extant population of *Asclepias purpurascens* on the Cape and the discovery of water hyacinth, *Eichhornia crassipes*, thriving in a spring upwelling near a Barnstable cranberry bog. Mario DiGregorio discussed, with a vial sample in hand, the group's discovery of a county record for *Wolffia papulifera* from a freshwater pond in Barnstable and showed images of sandplain grassland rarities: *Liatris scariosa* var. *novae-angliae* being visited by a monarch butterfly, *Aster concolor* at the northern limit of its range, *Aristida purpurascens*, New England's only perennial awngrass, and *Prenanthes serpentaria* from Nantucket. Pamela Polloni continued with the discussion of *P. serpentaria* by pointing out its hairy calyx, which distinguishes it from *P. trifoliata*, and other aspects of its life history such as pollination by *Bombus* bees and how to recognize the juvenile plants.

—Paul Somers, Recording Secretary.

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THE NEW ENGLAND BOTANICAL CLUB
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# RHODORA

## Journal of the New England Botanical Club

### CONTENTS

Inventory and vegetation classification of floodplain forest communities in Massachusetts. *Jennifer B. Kearsley* ........ 105

*Jaltomata lojae* (Solanaceae): Description and floral biology of a new Andean species. *Thomas Mione* and *Luis A. Serazo* ........ 136

The reproductive biology of *Magnolia grandiflora*. *Larry K. Allain, Michael S. Zavada,* and *Douglas G. Matthews* ........ 143

The taxonomy of *Carex* section *Scirpinae* (Cyperaceae). *Debra A. Dunlop* and *Garrett E. Crow* ........ 163

NEW ENGLAND NOTE

Rare and non-native plants of Massachusetts' floodplain forests. *Jennifer B. Kearsley* ........ 200

BOOK REVIEW

Wild Orchids Across North America: A Botanical Travelogue ........ 206

NEBC MEETING NEWS ........ 208

Information for Contributors ........ 213

NEBC Membership Form ........ 215

NEBC Officers and Council Members ........ inside back cover

MISSOURI BOTANICAL

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# INVENTORY AND VEGETATION CLASSIFICATION OF FLOODPLAIN FOREST COMMUNITIES IN MASSACHUSETTS

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JENNIFER B. KEARSLEY

Massachusetts Natural Heritage & Endangered Species Program,
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ABSTRACT. Floodplain forests on eleven rivers in Massachusetts were surveyed to determine the variation in vegetation and soils across a range of hydrologic, physiographic, and climatic conditions. Quantitative vegetation data collected from 124 plots at 43 sites were analyzed using TWINSPAN and DECORANA (DCA), and six community types were identified. The six types were: Type I—Riverine island floodplain forests (*Acer saccharinum–Populus deltoides–Acer negundo–Matteuccia struthiopteris* association); Type II—Major-river floodplain forests (*A. saccharinum–P. deltoides–Laportea canadensis* association); Type III—Transitional floodplain forests (*A. saccharinum–Arisaema dracontium* association); Type IV—Small-river floodplain forests (*A. saccharinum–Fraxinus pennsylvanica–Quercus palustris* association); Type V—Alluvial swamp forests (*Acer rubrum–A. saccharinum–Q. bicolor* association); and Type VI—Alluvial terrace forests (*A. rubrum–Carya ovata–Prunus serotina* association). The most common herbaceous taxa throughout all community associations were *M. struthiopteris, L. canadensis, Boehmeria cylindrica,* and *Onoclea sensibilis.* Results of the classification showed variation in floodplain forest vegetation composition among rivers in Massachusetts corresponding to significant differences in soil mottling, soil texture, presence/absence of a surface organic layer, and soil pH.

Key Words: *Acer saccharinum,* community classification, DECORANA, floodplain forest, Massachusetts, ordination, TWINSPAN

Floodplain forests, which develop on alluvial mineral soils within the zone of active flooding of rivers and streams, are considered to be among the most threatened, globally significant wetland community types in New England. Due to their high soil fertility and scenic qualities, floodplain forests have largely been converted to agriculture or lost to housing and industrial development. While several studies have addressed the relationship between floodplain forest vegetation and environmental variables within a single site or river basin in New England (Metzler and Damman 1985; Veneman and Tiner 1990), this study addresses the variability in floodplain forest vegetation and environments across river basins and physiographic regions. The objectives of the current study were to conduct a statewide vegetation classification of floodplain forest communities, to determine the distribution of defined community types across drainage basins and rivers, and to assess differences in environmental parameters among the identified floodplain forest community types.

The Massachusetts inventory and classification work is part of a regional effort to classify floodplain forests by state Natural Heritage Programs and The Nature Conservancy. Results of these projects will provide the baseline community data necessary for future in-depth studies of floodplain forest communities, and for land protection and conservation of these ecologically significant wetland communities.

## MATERIALS AND METHODS

**Site selection.** Potential floodplain forest sites were identified using USGS topographic quadrangles, Natural Resource Conservation Service soil surveys, and color-infrared (CIR) aerial photography. A combination of 1:25,000 scale, leaf-on CIR aerial photography from an unpublished community inventory of the Connecticut River Valley (Motzkin 1993), and 1:12,000 scale, leaf-off CIR aerial photography obtained from the Massachusetts Department of Environmental Protection Wetlands Conservancy Program were used. Potential floodplain forest sites were identified using the following criteria: (1) low, forested sections of greater than 3 ha occurring within 1–2 contour intervals (10–20 ft. elevation) of river's edge; (2) presence of alluvial soils; and (3) evidence of spring flooding and forest vegetation on aerial photography. The Massachusetts Natural Heritage and Endangered Species Program Biological and Conservation Database was also used to locate potential floodplain forest sites by identifying localities of tracked, state-protected rare species known to occur in floodplain forest habitats.

Using the resources and criteria listed above, 144 potential floodplain forest sites were identified in the state. Based on pre-

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Figure 1. Massachusetts' rivers and sub-ecoregions with sites surveyed for floodplain forest vegetation classification. Sub-ecoregions containing survey sites are shaded in grey.

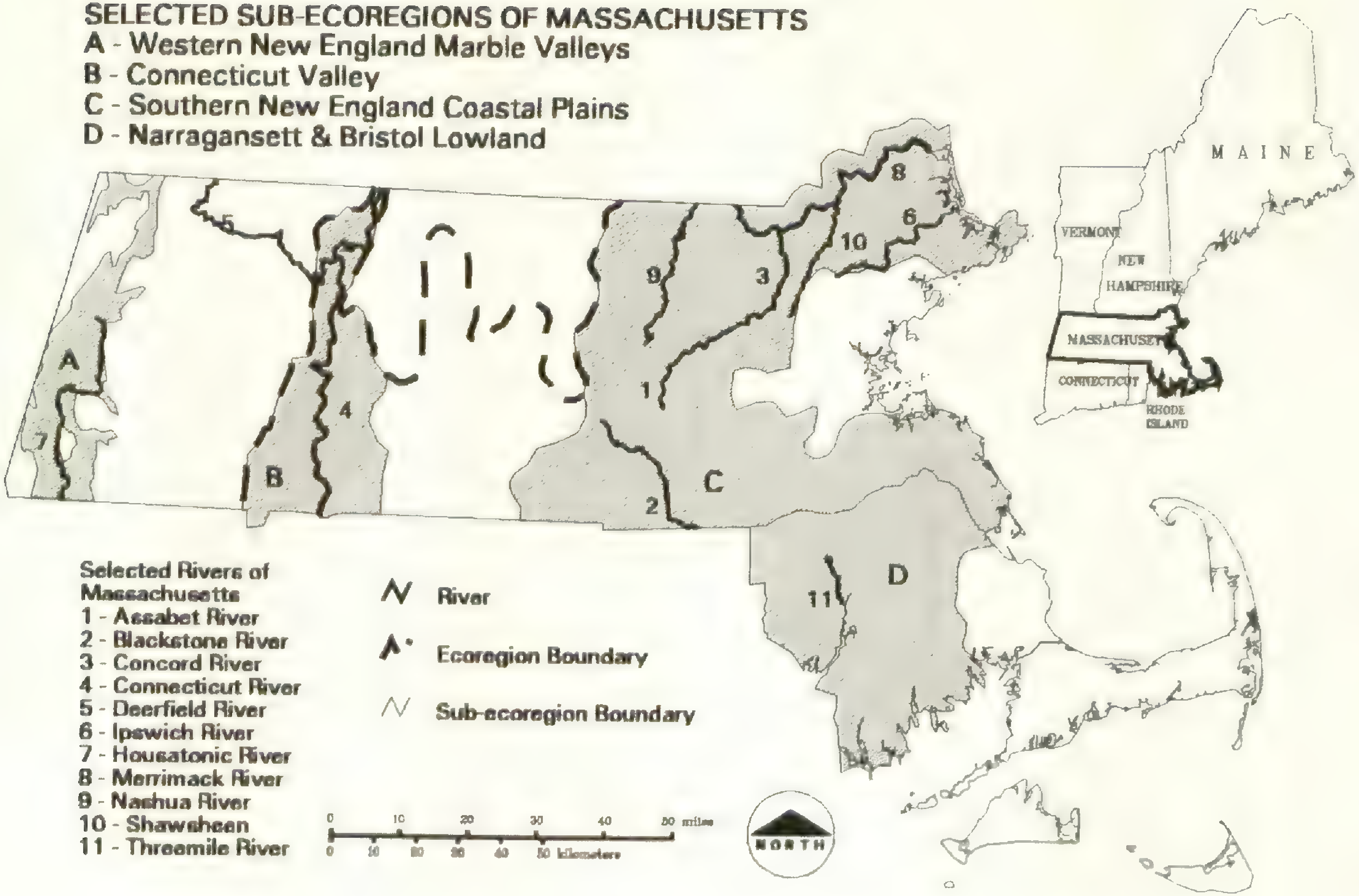
SELECTED SUB-ECOREGIONS OF MASSACHUSETTS
A - Western New England Marble Valleys
B - Connecticut Valley
C - Southern New England Coastal Plains
D - Narragansett & Bristol Lowland
Selected Rivers of Massachusetts
1 - Assabet River
2 - Blackstone River
3 - Concord River
4 - Connecticut River
5 - Deerfield River
6 - Ipswich River
7 - Housatonic River
8 - Merrimack River
9 - Nashua River
10 - Shawsheen
11 - Threemile River
River
Ecoregion Boundary
Sub-ecoregion Boundary
0 10 20 30 40 50 miles
0 10 20 30 40 50 kilometers
NORTH
MAINE
VERMONT
NEW HAMPSHIRE
MASSACHUSETTS
CONNECTICUT
RHODE ISLAND
A
B
C
D
1
2
3
4
5
6
7
8
9
10
11

Table 1. Drainage basins and river sections with sampled floodplain forest communities. Tributaries refer to third order or smaller streams. 50% Exceedance values indicate the discharge of 50% of flows annually, averaged over the period of record (Socolow et al. 1995). Exceedance values are given in cubic feet per second (cfs).

| Basin | River | Drainage Basin Area (sq. miles) | Mean 50% Exceedance (cfs) | Number of Sites | Number of Plots |
|---|---|---|---|---|---|
| Blackstone | Blackstone | 25.6 | 422 | 1 | 1 |
| Connecticut | Connecticut at Thompsonville, CT | 9,660 | 11,000 | 17 | 31 |
| | Connecticut tributaries | — | — | 7 | 24 |
| | Deerfield | 557 | 950 | 7 | 11 |
| Housatonic | Housatonic at Ashley Falls, MA | 465 | 456 | 5 | 13 |
| Ipswich | Ipswich | 44.5 | 37 | 1 | 4 |
| Merrimack | Assabet | 116 | 125 | 1 | 4 |
| | Concord | 400 | 481 | 1 | 4 |
| | Merrimack | 4,635 | 5,110 | 4 | 4 |
| | Nashua | 435 | 365 | 2 | 13 |
| | Nashua tributary | — | — | 1 | 3 |
| | Shawsheen | 36.5 | 38 | 2 | 6 |
| Taunton | Threemile | 84.3 | 113 | 1 | 6 |
| | | | Totals | 43 | 124 |

liminary field checks of potential sites, 55 were found to be semi-natural forested floodplain sites with evidence of periodic flooding (e.g. floodlines on trees, flood debris, or scoured surfaces) and a relative lack of evidence of human disturbance (e.g. limited clearings or non-native plant species). Quantitative vegetation and environmental data were collected at 43 of the semi-natural forested floodplain sites that were distributed across eleven rivers and four physiographic provinces, or sub-ecoregions (Figure 1).

The eleven rivers ranged in drainage basin area from 25–10,000 square miles, and in mean 50% exceedance values from 30–11,000 cubic feet per second (cfs; Table 1). Fifty percent exceedance values are used as indicators of average river discharge; they indicate the minimum discharge in cfs that 50% of all flows exceed annually, averaged over the period of record (Socolow et al. 1995). Identified floodplain forest sites ranged in size from 1 to 30 ha. Five sites less than the minimum size criterion of 3 ha were included because they either occurred on state-owned land with easy access (3 sites) or occurred on the Merrimack River (2 sites) where potential sampling sites were limited.

**Study area.** The eleven rivers sampled in this study are located within four subregions of the two ecological regions, or ecoregions, occurring in Massachusetts: the Northern Highlands Ecoregion and the Northeastern Coastal Zone (Figure 1; Griffith et al. 1994). These ecoregions are defined as areas with distinct geology, landforms, soils, vegetation, climate, wildlife, water, and human influences (Griffith et al. 1994).

The Northern Highlands Ecoregion includes all of Massachusetts west of the Connecticut River Valley and the Worcester Plateau in north-central Massachusetts as well as most of northern New England and the Adirondack Mountains in New York (Griffith et al. 1994). It roughly corresponds to the Adirondack–New England mixed forest–coniferous forest–alpine meadow province described by Bailey (1995). The Northeastern Coastal Zone includes eastern and coastal Massachusetts, most of southern New England, and coastal regions of New Hampshire and southern Maine (Griffith et al. 1994). It falls within the central Appalachian broadleaf forest–coniferous forest–meadow province described by Bailey (1995).

The lower Housatonic River runs through the Western New England Marble Valleys subregion of the Northern Highlands Ecoregion (Figure 1). Bedrock in this region, also known as the Berkshire Valley, consists of calcitic and dolomitic marbles and limestones; surface water alkalinity values in the area are high (>1000 μeq/L; Griffith et al. 1994). The Connecticut and Deerfield Rivers and the lower reaches of their tributaries are included in the Connecticut Valley subregion of the Northeastern Coastal Zone (Figure 1). The Connecticut Valley is characterized by thick outwash, alluvial, and lake bottom deposits overlaying sedimentary bedrock. Surface water alkalinity values are generally above 500 μeq/L.

The Blackstone, Concord, Assabet, Merrimack, Shawsheen, Ipswich, and Nashua Rivers occur within the Southern New England Coastal Plains and Hills subregion (Figure 1). This is the largest subregion in southern New England and is variable in its topography and bedrock. Bedrock types in the subregion are mostly granites, schist, and gneiss, and surface water alkalinity values are generally lower than in the Connecticut Valley, ranging from less than 50 to 500 μeq/L. The Threemile River occurs in the Narragansett Bristol Lowland subregion (Figure 1). The Narragansett Basin is similar to the Coastal Plains and Hills subregion, but bedrock outcrops are not common, and thick glacial till and outwash deposits cover the area. Surface water alkalinity values are generally between 100 to 300 μeq/L, but several areas have values less than 50 μeq/L (Griffith et al. 1994).

**Field methods.** Vegetation was sampled in 10 m × 20 m (0.02 ha) rectangular plots placed along transects perpendicular to the river. At most sites, two or more transects were placed at least 50 m apart. Each transect was walked and changes in topography and vegetation were described. A plot was placed within each identified topographic or vegetation unit. In small floodplain forests (≤3 ha), one or two plots were subjectively placed within the "typical" vegetation type(s) and not along transects. The number of plots per site ranged from 1 at small sites to 8 at large sites.

Plots were placed with their long axis parallel to the river. Percent cover of trees (stems >10 cm DBH), shrubs (stems <10 cm DBH), saplings, and vines was visually estimated within each 0.02 ha plot, and percent cover of herbs and seedlings was visually estimated within two 0.0004 ha (2 m × 2 m) square subplots. Herbaceous taxa (<1 m tall) occurring within the 0.02 ha plot, but not within the subplots, were also recorded. Nomenclature follows Kartesz (1994). Percent cover for all taxa was estimated using a modified Braun-Blanquet cover scale with the following cover classes: r (single occurrence), <1%, 1–5%, 6–10%, 11–20%, 21–25%, 26–35%, 36–45%, 46–50%, 51–55%, 56–65%, 66–75%, 76–85%, 86–95%, and 96–100%. The average height and average percent cover of each vegetation stratum were also visually estimated and recorded.

Vegetation data from 124 plots were included in the vegetation classification (Table 1). Eighty-nine plots were surveyed between July and September, 1997, using the methods described above. Existing data from 35 plots collected with equivalent methodologies by other sources were included in the vegetation classification. Those data were: 10 plots from the Deerfield River (Thompson and Jenkins 1992), 16 plots from the Nashua River

(Searcy et al. 1993), 7 plots from the Connecticut River and its tributaries (Motzkin 1993, 1995; Massachusetts Audubon Society, unpubl. data), and 2 plots from the Ipswich River (Massachusetts Audubon Society, unpubl. data).

Environmental data were collected from the 89 plots sampled in 1997. At each plot, one 60 cm deep soil pit was dug and the following soil characteristics were described: depth, soil texture, and color of horizons; depth to mottling; color of mottles; depth of root penetration; and average pH of the mineral soil. The following environmental data were also collected for each plot: topographic position (terrace, levee, level floodplain, depression), height of floodlines, and the number of stumps, and uprooted and snapped trees. Any evidence of disturbance or land use was also noted.

**Data analysis.** Vegetation cover data were analyzed using two-way indicator species analysis (TWINSPAN) and ordination techniques (DCA) contained in the PC-ORD Version 3.0 statistical package (McCune and Mefford 1997). TWINSPAN (Hill 1979a) was used to identify floodplain forest types, and DCA (Hill 1979b) was used to illustrate the relationship between types. Default settings were used with the following exceptions: Braun-Blanquet cut-levels (0, 5, 26, 51, and 76) were used in the TWINSPAN analysis, and downweighting of rare species was used in DCA. Community types were based on both TWINSPAN and DCA results. Species indicator values for the community types were calculated using the Indicator Species Method of Dufrêne and Legendre (1997) in the PC-ORD Version 3.0 statistical package (McCune and Mefford 1997). Indicator species defined by the Indicator Species Method were used instead of TWINSPAN indicator species to describe community types because: (1) final community types were based on both TWINSPAN and DCA results, and (2) the Indicator Species Method defines indicator species as those species present in the majority of sites belonging to a group, while TWINSPAN defines them as those species that are found mostly in a single group, but not necessarily in the majority of that group's sites (Dufrêne and Legendre 1997). A Monte Carlo technique was used to test for the statistical significance of indicator values.

Species richness, evenness (E), and Shannon diversity index (H′) values were calculated for each plot using the method outlined in the PC-ORD statistical package (McCune and Mefford 1997). Single factor analysis of variance (ANOVA) was used to test if the indices were significantly different among community types. A multi-response permutation procedure (MRPP; Zimmerman et al. 1985) was used to test if defined community types differed significantly in height and total percent cover of the following six strata: emergent canopy, tree canopy, tree sub-canopy, tall shrubs, short shrubs, and herbs.

In order to test for differences in soil characteristics among the defined community types, an MRPP was run on the following variables: presence/absence of soil mottling, depth to mottling (cm), soil texture at 10 cm intervals (sand, loamy sand, sandy loam, and silt loam), presence/absence of a surface organic layer, depth of organic layer, pH, and presence/absence of hydric soil. Hydric soil determination was based on the criteria outlined by the Natural Resource Conservation Service (1994). Individual ANOVA and chi-square tests were used to determine which soil variables were significantly different (at $p < 0.01$) among defined community types. Chi-square tests were used to test for significant differences in presence/absence of floodlines and topographic position.

## RESULTS

**Vegetation classification.** Six vegetation community types were recognized based on the TWINSPAN (Figure 2) and DCA (Figure 3) results. There was general agreement between TWINSPAN groups and DCA output (Figure 3). The six community types described below are primarily based on the TWINSPAN output (Figure 2) with two exceptions. First, twelve plots classified as one type by the TWINSPAN analysis were moved to a different community type based on the DCA results. For example, TWINSPAN classified ten plots as Type I (Figure 2), but the DCA results showed that two plots classified as Type II by TWINSPAN were more closely related to plots classified as Type I. Therefore, Type I is described below as containing twelve plots, and twelve plots were included in the environmental analyses. The second exception is that four plots classified by TWINSPAN were eliminated from the final community types described below and from the environmental analyses because they were found to be distinct species assemblages, unlike all other plots.

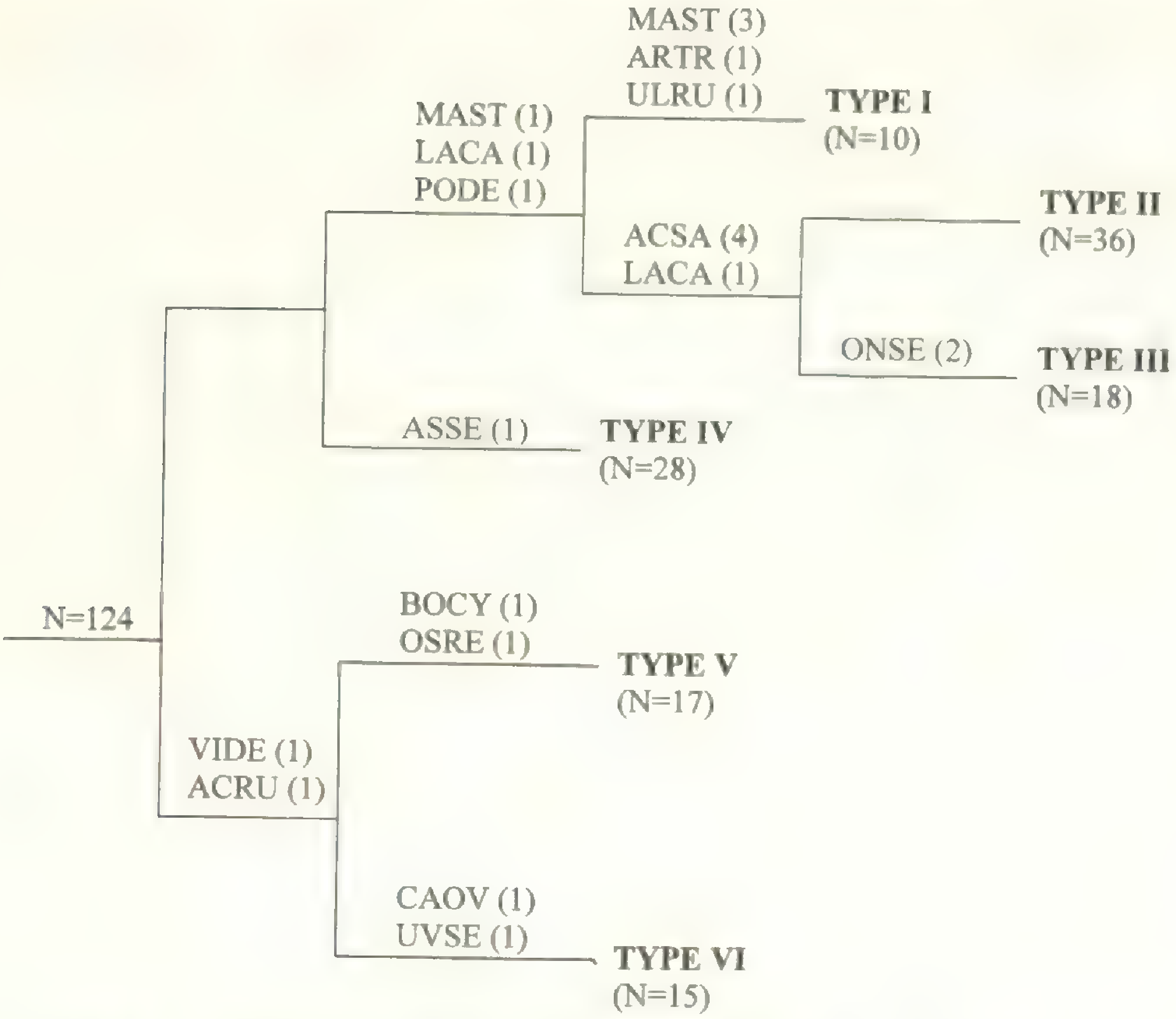
MAST (3)
ARTR (1)
ULRU (1)
TYPE I
(N=10)
MAST (1)
LACA (1)
PODE (1)
TYPE II
(N=36)
ACSA (4)
LACA (1)
ONSE (2)
TYPE III
(N=18)
ASSE (1)
TYPE IV
(N=28)
N=124
BOCY (1)
OSRE (1)
TYPE V
(N=17)
VIDE (1)
ACRU (1)
CAOV (1)
UVSE (1)
TYPE VI
(N=15)

Figure 2. TWINSPAN dendrogram of floodplain forest community types with TWINSPAN indicator species listed at divisions. Species codes follow those listed in Table 2. Numbers in parentheses next to each species indicate the minimum percent cover class for that species in all plots within the community type: (1) 0–4%, (2) 5–25%, (3) 26–50%, (4) 51–75%. Sample sizes refer to the number of plots classified as each type in the TWINSPAN analysis.

The primary division of plots in TWINSPAN was made based on the occurrence of *Acer saccharinum* and *A. rubrum* with Types I, II, III, and IV having *A. saccharinum* dominant in the overstory and Types V and VI having *A. rubrum* dominant (Figure 2). Variation in species composition across DCA ordination Axis 1 ($R^2 = 0.227$) was also associated with a decrease in *A. saccharinum* and increase in *A. rubrum.* Variation in species composition across DCA Axis 2 ($R^2 = 0.127$) was associated with an increase in *Ulmus rubra* and *Impatiens pallida* and a decrease in *Populus deltoides* and *Laportea canadensis.* Axis 3 did not characterize much additional variation in species composition ($R^2 = 0.038$). Plots of Types II and III were closely related in TWINSPAN

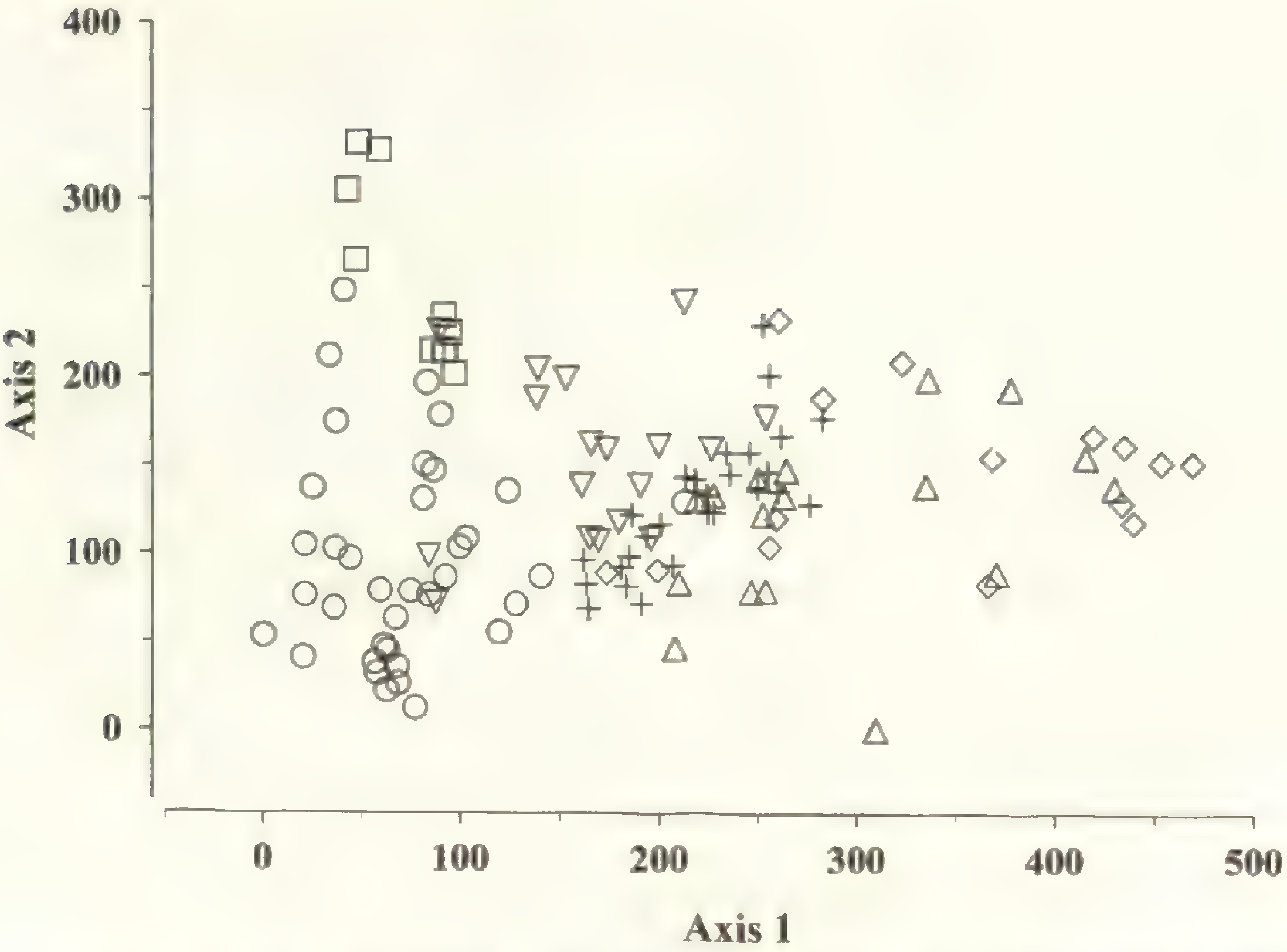

Figure 3. First two axes of the floodplain forest DCA output with plots coded by TWINSPAN group. Squares = Type I, circles = Type II, down-facing triangles = Type III, pluses = Type IV; up-facing triangles = Type V, and diamonds = Type VI.

clustering where they divided at the fourth division (Figure 2), but they were well separated in the DCA analysis along both Axes 1 and 2 (Figure 3).

Two hundred and fourteen vascular plant species were identified in the floodplain forest sampling. A subset of those species with indicator values that were significant ($p \leq 0.05$) and/or greater than 10% are listed in Table 2. Indicator values represent a combination of species relative abundance and relative frequency of occurrence in the identified community types (Dufrêne and Legendre 1997). For example, an indicator value of 10% assumes that the species was present in at least 33% of sites in a community type, and that the relative abundance of the species was at least 33% in one of the community types. If one of the two measures was 100% then the other was at least 10% (Dufrêne and Legendre 1997). Thirty-four taxa with indicator values greater than 20% were plotted according to their DCA axis loading scores for Axis 1 and Axis 2 to illustrate the relationship between species abundance and community types (Figure 4).

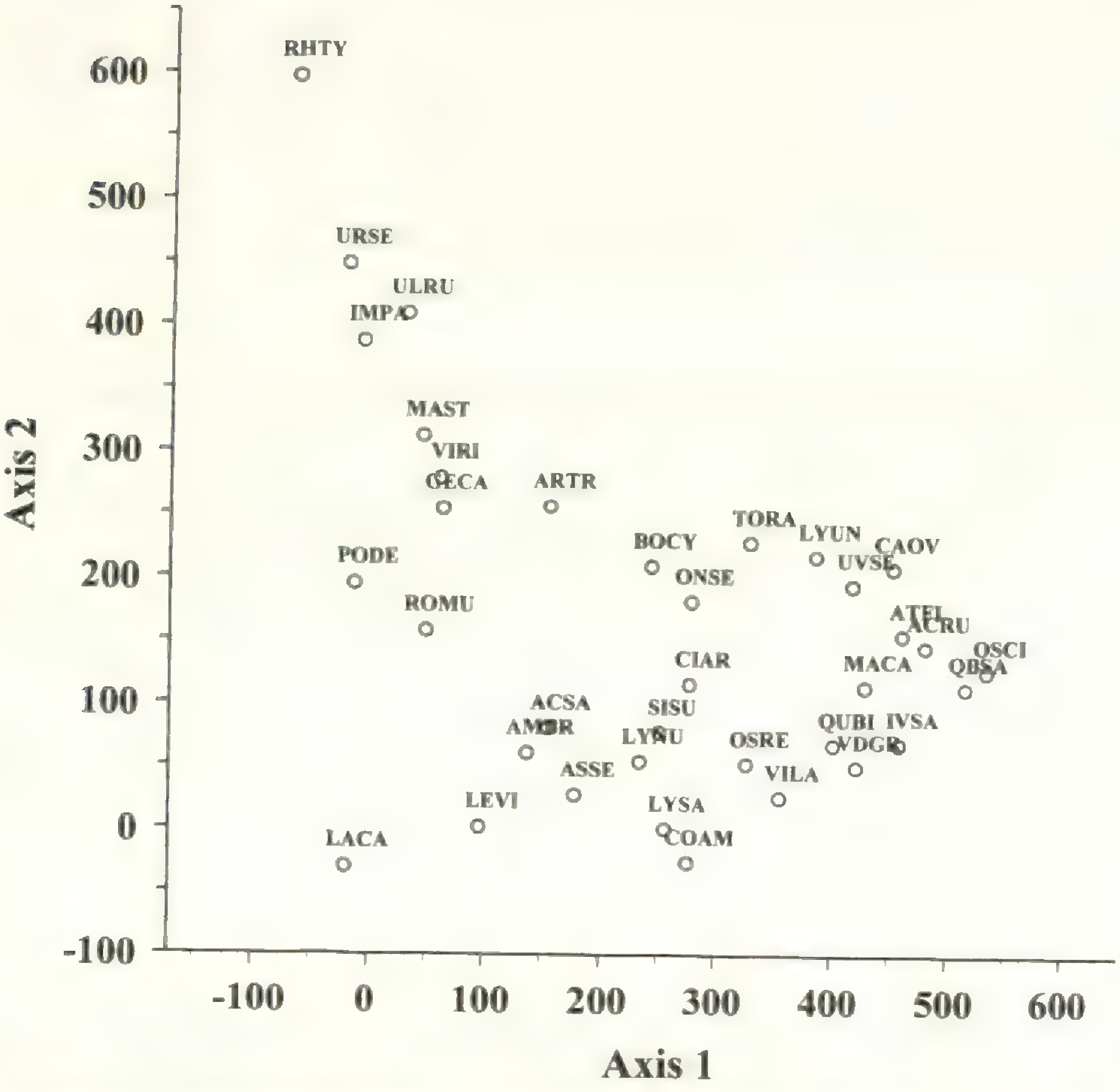

Figure 4. Floodplain forest species with indicator values that are >20% and significant ($p \leq 0.05$) plotted by their axis loading scores for DCA Axis 1 and Axis 2.

*Acer saccharinum* was the most common tree species encountered and therefore had a low maximum indicator value (22%) for any single community type (Table 2). *Acer saccharinum* attained its highest indicator values in Types II (20%), III (20%), and IV (22%). *Ulmus rubra* was a strong indicator species (46%) for Type I, *Populus deltoides* for Types I and II (24% and 28%, respectively), and *A. rubrum* and *Carya ovata* for Type VI (60% and 49%, respectively; Table 2). Shrubs and saplings were important components of Types I, V, and VI: *Berberis thunbergii, Rhus typhina,* and *Rosa multiflora* had high indicator values in Type I floodplain forests; *Cornus amomum* and *Rhamnus frangula* in Type V; and *Ilex verticillata, Viburnum dentatum,* and *Quercus bicolor* seedlings in Type VI (Table 2; Figure 4).

Table 2. Indicator values and associated $p$ values for floodplain forest taxa listed by community type. * indicates non-native species.

| Species Name | CODE | Indicator Values by Community Type | | | | | | $p$ value |
|---|---|---|---|---|---|---|---|---|
| | | I | II | III | IV | V | VI | |
| *Acer saccharinum* | ACSA | 10 | 20 | 20 | 22 | 14 | 1 | 0.035 |
| TYPE I | | | | | | | | |
| *Matteuccia struthiopteris* | MAST | 61 | 10 | 15 | 0 | 0 | 0 | 0 |
| *Ulmus rubra* | ULRU | 46 | 3 | 0 | 0 | 0 | 0 | 0 |
| *Impatiens pallida* | IMPA | 38 | 2 | 0 | 0 | 0 | 0 | 0 |
| *Arisaema triphyllum* | ARTR | 33 | 6 | 11 | 2 | 0 | 4 | 0 |
| *U. rubra* seedling | URSE | 31 | 0 | 0 | 0 | 0 | 0 | 0 |
| *A. negundo* sapling | ANSA | 25 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Rhus typhina* | RHTY | 25 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Vitis riparia* | VIRI | 25 | 1 | 7 | 0 | 0 | 0 | 0.017 |
| **Berberis thunbergii* | BETH | 24 | 0 | 0 | 0 | 0 | 0 | 0.006 |
| *A. negundo* seedlings | ANSE | 22 | 0 | 0 | 0 | 0 | 0 | 0.001 |
| **Rosa multiflora* | ROMA | 20 | 2 | 0 | 0 | 0 | 0 | 0.027 |
| *Geum canadense* | GECA | 18 | 3 | 8 | 0 | 0 | 0 | 0.031 |
| *Acer negundo* | ACNE | 16 | 3 | 0 | 0 | 0 | 0 | 0.042 |
| **Celastrus orbiculata* | CEOR | 10 | 3 | 1 | 3 | 0 | 0 | 0.26 |
| *Eupatorium rugosum* | EURU | 10 | 6 | 9 | 0 | 0 | 0 | 0.437 |
| TYPE II | | | | | | | | |
| *Laportea canadensis* | LACA | 0 | 84 | 3 | 0 | 0 | 0 | 0 |
| *Leersia virginica* | LEVI | 0 | 29 | 19 | 2 | 2 | 0 | 0.058 |
| *Populus deltoides* | PODE | 24 | 28 | 1 | 0 | 0 | 0 | 0.001 |
| *Helianthus tuberosus* | HETU | 0 | 15 | 0 | 0 | 0 | 0 | 0.046 |

Table 2. Continued.

| Species Name | CODE | Indicator Values by Community Type | | | | | | p value |
|---|---|---|---|---|---|---|---|---|
| | | I | II | III | IV | V | VI | |
| **Glechoma hederacea* | GLHE | 1 | 14 | 1 | 0 | 0 | 0 | 0.214 |
| **Chelindonium majus* | CHMA | 0 | 13 | 0 | 0 | 0 | 0 | 0.073 |
| TYPE III | | | | | | | | |
| *Boehmeria cylindrica* | BOCY | 0 | 1 | 32 | 24 | 20 | 0 | 0.013 |
| *Cinna arundinacea* | CIAR | 0 | 2 | 32 | 1 | 11 | 0 | 0.015 |
| *Onoclea sensibilis* | ONSE | 1 | 0 | 27 | 25 | 13 | 7 | 0.013 |
| *Toxicodendron radicans* | TORA | 0 | 1 | 25 | 9 | 18 | 15 | 0.127 |
| *Amphicarpaea bracteata* | AMBR | 0 | 2 | 24 | 1 | 0 | 0 | 0.002 |
| *U. americana* sapling | UASA | 0 | 2 | 20 | 0 | 0 | 1 | 0.054 |
| **Alliaria petiolata* | ALOF | 0 | 2 | 18 | 0 | 0 | 0 | 0.054 |
| *Arisaema dracontium* | ARDR | 0 | 0 | 16 | 0 | 0 | 0 | 0.011 |
| *Polygonum virginianum* | TOVI | 1 | 2 | 16 | 0 | 0 | 0 | 0.026 |
| *F. americana* sapling | FASA | 0 | 0 | 14 | 0 | 0 | 0 | 0.045 |
| *A. saccharinum* sapling | ASSA | 2 | 4 | 13 | 3 | 1 | 0 | 0.21 |
| *Platanus occidentalis* | PLOC | 2 | 0 | 12 | 0 | 0 | 0 | 0.05 |
| TYPE IV | | | | | | | | |
| *A. saccharinum* seedlings | ASSE | 0 | 1 | 0 | 39 | 8 | 0 | 0.001 |
| *Sium suave* | SISU | 0 | 0 | 0 | 29 | 0 | 0 | 0 |
| **Lysimachia nummularia* | LYNU | 0 | 0 | 0 | 23 | 0 | 0 | 0.026 |
| *F. pennsylvanica* seedlings | FPSE | 9 | 0 | 0 | 20 | 0 | 0 | 0.016 |
| *Cephalanthus occidentalis* | CEOC | 0 | 0 | 0 | 19 | 1 | 0 | 0.01 |

Table 2. Continued.

| Species Name | CODE | Indicator Values by Community Type I | II | III | IV | V | VI | *p* value |
|---|---|---|---|---|---|---|---|---|
| *Fraxinus pennsylvanica* | FRPE | 0 | 0 | 1 | 19 | 6 | 1 | 0.039 |
| *Lysimachia terrestris* | LYTE | 0 | 0 | 0 | 18 | 0 | 2 | 0.012 |
| *Quercus palustris* | QUPA | 0 | 0 | 0 | 18 | 0 | 0 | 0.007 |
| **Myosotis scorpioides* | MYSC | 0 | 0 | 0 | 17 | 0 | 0 | 0.043 |
| *Cicuta maculata* | CIMA | 0 | 0 | 0 | 14 | 0 | 0 | 0.035 |
| *Leersia oryzoides* | LEOR | 0 | 0 | 0 | 14 | 0 | 0 | 0.029 |
| *Q. palustris* seedlings | QPSE | 0 | 0 | 0 | 14 | 0 | 0 | 0.055 |
| *Phalaris arundinacea* | PHAR | 0 | 0 | 0 | 13 | 0 | 0 | 0.035 |
| **Polygonum persicaria* | PLRS | 0 | 0 | 1 | 13 | 0 | 0 | 0.139 |
| *Carex lupulina* | CALU | 0 | 0 | 0 | 11 | 0 | 0 | 0.065 |
| *Carex typhina* | CATY | 0 | 0 | 0 | 11 | 0 | 0 | 0.079 |
| *Lobelia cardinalis* | LOCA | 0 | 0 | 0 | 11 | 0 | 0 | 0.078 |
| TYPE V | | | | | | | | |
| *Osmunda regalis* | OSRE | 0 | 0 | 0 | 0 | 53 | 0 | 0 |
| *Quercus bicolor* | QUBI | 0 | 0 | 0 | 0 | 39 | 4 | 0 |
| *Vitis labrusca* | VILA | 0 | 0 | 0 | 0 | 31 | 0 | 0 |
| **Lythrum salicaria* | LYSA | 0 | 0 | 0 | 6 | 25 | 0 | 0.003 |
| *Cornus amomum* | COAM | 0 | 0 | 0 | 6 | 24 | 3 | 0.013 |
| *Lycopus uniflorus* | LYUN | 0 | 0 | 0 | 0 | 20 | 0 | 0.003 |
| *Carex crinita* | CACR | 0 | 0 | 0 | 9 | 15 | 0 | 0.095 |
| **Rhamnus frangula* | RHFR | 0 | 0 | 0 | 3 | 15 | 6 | 0.047 |
| *Betula nigra* | BENI | 0 | 0 | 0 | 4 | 13 | 0 | 0.042 |
| *Q. bicolor* seedlings | QBSE | 0 | 0 | 0 | 0 | 13 | 8 | 0.067 |

Table 2. Continued.

| Species Name | CODE | Indicator Values by Community Type I | II | III | IV | V | VI | *p* value |
|---|---|---|---|---|---|---|---|---|
| TYPE VI | | | | | | | | |
| *Acer rubrum* | ACRU | 0 | 0 | 0 | 0 | 13 | 60 | 0 |
| *Viburnum dentatum* | VIDE | 0 | 0 | 0 | 0 | 16 | 54 | 0 |
| *Carya ovata* | CAOV | 0 | 0 | 0 | 0 | 0 | 49 | 0 |
| *Ilex verticillata* | ILVE | 0 | 0 | 0 | 1 | 0 | 47 | 0 |
| *Athyrium felix-femina* | ATFI | 0 | 0 | 0 | 0 | 1 | 37 | 0 |
| *Maianthemum canadense* | MACA | 0 | 0 | 0 | 0 | 3 | 37 | 0 |
| *Uvularia sessilifolia* | UVSE | 0 | 0 | 0 | 0 | 0 | 35 | 0 |
| *Osmunda cinnamomea* | OSCI | 0 | 0 | 0 | 0 | 0 | 29 | 0 |
| *Q. bicolor* saplings | QBSA | 0 | 0 | 0 | 0 | 0 | 21 | 0.003 |
| *Tilia americana* | TIAM | 1 | 0 | 0 | 0 | 0 | 19 | 0.004 |
| *P. serotina* seedlings | PSSE | 0 | 0 | 0 | 0 | 0 | 14 | 0.017 |
| *Ulmus americana* | ULAM | 2 | 2 | 2 | 1 | 6 | 12 | 0.308 |
| *Circaea lutetiana* ssp. *canadensis* | CIQU | 4 | 1 | 1 | 0 | 1 | 11 | 0.206 |
| *Parthenocissus quinquefolia* | PAQU | 3 | 4 | 0 | 3 | 0 | 11 | 0.825 |
| *A. rubrum* seedlings | ARSE | 0 | 0 | 0 | 1 | 0 | 10 | 0.068 |
| *Prunus serotina* | PRSE | 4 | 0 | 0 | 0 | 5 | 6 | 0.511 |

Variation in abundance of woody vines along DCA Axis 1 was associated with an increase in *Vitis labrusca* and a decrease in *V. riparia* (Figure 4); *V. labrusca* attained its highest indicator value in Type V, while *V. riparia* was most abundant in Type I (Table 2). *Toxicodendron radicans* occurred across all plots, but was most abundant in Types III, IV, V, and VI (Table 2). Variation in herbaceous species composition across DCA Axis 1 was associated with a decrease in *Matteuccia struthiopteris* and *Laportea canadensis* and an increase in *Osmunda regalis* and *O. cinnamomea* (Figure 4). *Boehmeria cylindrica* and *Onoclea sensibilis* had intermediate Axis 1 loading scores (Figure 4) and high indicator values for Types III, IV, and V (Table 2). Variation in herbaceous species composition across Axis 2 was associated with decreasing *L. canadensis* and increasing *Impatiens pallida* and *M. struthiopteris* (Figure 4).

Community structure was similar among floodplain forest types, and the six community types did not differ significantly in the height and total percent cover of vegetation strata (MRPP $p = 0.45$). All types were characterized by a dense, tall tree canopy (20 m mean height, 70% mean cover) above a diffuse subcanopy (7 m mean height, 19% mean cover) and very limited to absent shrub layer (1.5 m mean height, 9% mean cover). The herbaceous cover was dense (80% mean cover) in most plots, and tall (1–2 m) when *Laportea canadensis* or *Impatiens* spp. were dominant (Types I and II; Table 2). Species richness was not significantly different among identified types ($p = 0.217$), but types did differ significantly in species diversity ($p = 0.029$) and species evenness ($p = 0.0004$) with Type VI forests having the highest values for both ($H' = 1.75$, $E = 0.71$).

**Environmental parameters.** Soil profiles of Types III, IV, V, and VI were typically hydric silt loams with soil mottling, while soil profiles of Types I and II were nonhydric, sandy loams, loamy sands, or sands without soil mottling (Table 3). Soil profiles of Types V and VI usually had a surface organic layer, while soil profiles of Types I, II, and III usually lacked a surface organic layer (Table 3). Soil pH was least acidic in Types I, II, and III (Table 3).

Results of the MRPP of soil variables showed that the observed differences in soil profiles among the six floodplain forest community types were statistically significant ($p = 0.001$). Soil texture, pH, and presence/absence of soil mottles, surface organic layer, and hydric soils were all significantly different ($p < 0.001$) among community types, while depth to mottling and depth of organic layer were not significantly different (Table 3).

Presence/absence of floodlines and topographic position were also significantly different among defined types ($p < 0.001$). Most floodplain plots occurred on level floodplains, except for Type I communities which typically occurred on elevated sections of riverine islands and Type VI communities which occurred on ridges or high terraces (Table 3). Floodlines were visible on tree trunks in 41% of all plots, and they were most common in community Types III and IV (Table 3). Snapped trunks were observed in 34% of all plots, uprooted trunks in 7%, and stumps (cut or beaver-cut) in 16%. When present, there were usually only one or two downed trees per 0.02 ha plot, and downed trees did not appear to be abundant overall in the floodplain forests inventoried.

## COMMUNITY TYPE DESCRIPTIONS

**Type I—Riverine island floodplain forests (*Acer saccharinum–Populus deltoides–Acer negundo–Matteuccia struthiopteris* association).** Type I communities (12 plots at 8 sites) were open-canopy floodplain forests occurring on elevated sections of riverine islands and riverbanks of major rivers with high levels of disturbance. The community type was limited to the Connecticut, Deerfield, and Housatonic Rivers in Massachusetts (Table 4). Plots classified as Type I were most likely to occur at sites where the vegetation in all plots at the site was classified as Type I. Table 5 shows that of the eight sites with plots classified as Type I, five had all plots classified as Type I, three had plots classified as both Types I and II, and one had plots classified as Types I, II, and III. Type I communities were never associated at sites with vegetation classified as Types IV, V, or VI (Table 5). Soils of Type I communities were typically nonhydric, sandy loams without soil mottles and without a surface organic layer. Soil pH ranged from 5.5 on the Connecticut and Deerfield River plots to 8.0 on the Housatonic River (Table 3).

The overstory of Type I communities was a mixture of *Acer saccharinum* and *Populus deltoides. Platanus occidentalis* and

Table 3. Environmental data for floodplain forest community types. *Soil texture: S = Sand, LS = Loamy Sand, SL = Sandy Loam, ST = Silt Loam. **Topographical position of plots within floodplain: TR = Terrace, LF = Level Floodplain, LE = Levee, DP = Depression.

| Type | Number of Plots | % of Plots with Soil Mottling (mean depth to, in cm) | % of Plots with each *Soil Texture at 10 cm | | | | % of Plots with Soil Organic Layer (mean depth of, in cm) | Mean pH (range) | % of Plots with Hydric Soil | % of Plots with Floodlines (height range in cm) | % of Plots in each **Topographical Position | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | S | LS | SL | ST | | | | | TR | LF | LE | DP |
| I | 11 | 0 | 0 | 0 | 91 | 9 | 0 | 6.6 (5.5–8.0) | 0 | 36 (43–135) | 64 | 27 | 9 | 0 |
| II | 23 | 13 (15.7) | 5 | 14 | 50 | 31 | 4 (1.0) | 6.3 (4.5–8.0) | 0 | 13 (93–220) | 13 | 61 | 26 | 0 |
| III | 16 | 75 (18.3) | 0 | 6 | 31 | 63 | 0 | 6.2 (4.5–8.0) | 38 | 62 (60–303) | 19 | 75 | 0 | 6 |
| IV | 16 | 88 (14.0) | 6 | 6 | 12 | 76 | 35 (5.0) | 5.2 (4.5–6.0) | 59 | 69 (44–265) | 0 | 94 | 6 | 0 |
| V | 17 | 67 (26.1) | 0 | 6 | 27 | 67 | 67 (5.0) | 4.8 (4.5–5.5) | 40 | 47 (45–122) | 0 | 80 | 7 | 13 |
| VI | 5 | 60 (17.3) | 0 | 0 | 40 | 60 | 60 (5.3) | 5.0 (4.5–6.0) | 40 | 0 | 60 | 40 | 0 | 0 |
| ALL | 87 | 50 (18.5) | 2 | 5 | 42 | 51 | 23 (4.8) | 5.7 (4.5–8.0) | 30 | 41 (43–303) | 19 | 73 | 10 | 3 |

Table 4. Number of plots by each river in the defined floodplain forest community types.

| | | Community Type | | | | | |
|---|---|---|---|---|---|---|---|
| Basin | River | I | II | III | IV | V | VI |
| Blackstone | Blackstone | | | | | | 1 |
| Connecticut | Connecticut | 9 | 20 | 1 | | | |
| | Connecticut tributaries | | 1 | 9 | 12 | | 2 |
| | Deerfield | 2 | 8 | 1 | | | |
| Housatonic | Housatonic | 1 | 3 | 8 | | | |
| Ipswich | Ipswich | | | | 4 | | |
| Merrimack | Assabet | | | | 1 | 2 | 1 |
| | Concord | | | | | 4 | |
| | Merrimack | | | | 2 | | |
| | Nashua | | | | 1 | 3 | 9 |
| | Nashua tributary | | | | 3 | | |
| | Shawsheen | | | | 2 | 4 | |
| Taunton | Threemile | | | | 3 | 2 | 1 |
| | Totals | 12 | 32 | 19 | 28 | 15 | 14 |

*Fraxinus americana* were occasional canopy associates. *Ulmus rubra, A. negundo,* and *Celtis occidentalis* (on the Housatonic River) were common in the subcanopy (Table 2). The shrub/sapling layer was patchy and composed of taxa typical of disturbed areas, including *Rhus typhina, Rosa multiflora, Berberis thunbergii,* and *Celastrus orbiculata. Berberis thunbergii* was observed in this floodplain forest community type more frequently than in any other (Table 2). The herb layer was dominated by *Matteuccia struthiopteris* (most plots had greater than 40% cover) or by a

Table 5. Number of sites with plots of one defined floodplain forest community type that also have plots of other community types.

| | Type I | Type II | Type III | Type IV | Type V | Type VI | Total # of Sites with Plots of Type |
|---|---|---|---|---|---|---|---|
| Type I | 5 | 3 | 1 | | | | 8 |
| Type II | 3 | 7 | 7 | | | | 17 |
| Type III | 1 | 7 | 3 | 1 | | | 11 |
| Type IV | | | 1 | 7 | 4 | 3 | 12 |
| Type V | | | | 4 | 2 | 3 | 6 |
| Type VI | | | | 3 | 3 | 2 | 5 |

dense, tall layer of *Impatiens pallida* over *M. struthiopteris. Laportea canadensis* occurred in low amounts but was never abundant. Other common herbaceous taxa were *Eupatorium rugosum, Arisaema triphyllum,* and *Geum canadense. Vitis riparia* was a strong indicator vine (Table 2), and *Parthenocissus quinquefolia* was also common.

**Type II—Major-river floodplain forests (*Acer saccharinum–Populus deltoides–Laportea canadensis* association).** Type II communities (32 plots at 17 sites) occurred on mainstem sections of the Connecticut, Deerfield, and Housatonic Rivers (Table 4). Plots classified as Type II were most likely to occur at sites with other plots classified as Type II or at sites with plots classified as Type III (Table 5). Type II communities sometimes occurred associated with vegetation classified as Type I, but never with Types IV, V, or VI (Table 5). Soils were predominantly sandy loams without soil mottles (13% of plots had mottles) and without a surface organic layer (only 4% of plots had an organic layer). Soil pH ranged from 4.5 on the Connecticut and Deerfield Rivers to 8.0 on the Housatonic (Table 3).

*Acer saccharinum* was strongly dominant in the overstory (>60% cover in most plots) mixed with lesser amounts of *Populus deltoides. Ulmus americana* and/or *U. rubra* occurred in the subcanopy. Shrubs were generally lacking. The herbaceous layer was usually dominated by a 1–2 m tall, dense cover of *Laportea canadensis,* and *Matteuccia struthiopteris* was sometimes abundant. *Leersia virginica* was consistently represented, but in low amounts (typically <5% cover). Other common associates were *Cinna arundinacea, Impatiens* sp., *Boehmeria cylindrica,* and *Arisaema triphyllum.* Non-native plant species were usually less abundant than in Type I communities, but *Polygonum cuspidatum* often formed large patches along heavily scoured levees or in areas where the canopy was open. Other common non-native taxa were *Glechoma hederacea* and *Alliaria petiolata.*

**Type III—Transitional floodplain forests (*Acer saccharinum–Arisaema dracontium* association).** Type III communities (19 plots at 11 sites) occurred on third-order or smaller tributaries of the Connecticut River, on the Housatonic River, and in depressions within Major-river floodplain forests (Types I and II) of the Connecticut and Deerfield Rivers (Table 4). Plots classified as Type III were found associated at sites with plots classified as Types I, II, and IV (Table 5). Type III communities were intermediate in soil texture and drainage between the sandy, well-drained soils of Types I and II and the highly mottled, poorly drained silt loams of Type IV. Soil texture was silt loam or very fine sandy loam. Soils were poorly drained, and 75% of plots had soil mottling. None of the plots had a surface organic layer. The pH ranged from 4.5 to 8.0 (Table 3).

The Type III vegetation association was transitional between Major-river (Types I, II) and Small-river (Type IV) floodplain forest vegetation, and shared taxa with Types I, II and IV (Table 2; Figure 3). In Type III communities, *Acer saccharinum* was dominant in the canopy, but unlike Types I and II, *Populus deltoides* was typically absent. As in Type IV plots, *Fraxinus pennsylvanica* and *Ulmus americana* were present. A shrub layer was lacking; however, saplings of overstory trees were common. Vines were abundant with *Amphicarpaea bracteata* most common. In contrast to Type II plots, *Laportea canadensis* was not dominant, but it was present in low amounts in all plots (5–15% cover). The herbaceous layer was typically an even mixture of *L. canadensis, Matteuccia struthiopteris, Onoclea sensibilis,* and *Boehmeria cylindrica.* Common associates were *Leersia virginica, Arisaema triphyllum, Bidens frondosa, Cinna arundinacea,* and *Impatiens* sp. *Arisaema dracontium* (a state-protected rare species) was associated with this floodplain forest community type and serves as a good indicator species of the type (Indicator value = 16; Table 2; Kearsley 1999).

**Type IV—Small-river floodplain forests (*Acer saccharinum–Fraxinus pennsylvanica–Quercus palustris* association).** Type IV communities (28 plots at 12 sites) occurred on third order or smaller tributaries of the Connecticut and Nashua Rivers, on smaller rivers of eastern Massachusetts where banks are low and overbank flooding occurs (Ipswich, Assabet, Shawsheen, and Threemile), and on edges of riverine islands of the Merrimack River (Table 4). Vegetation classified as Type IV was sometimes associated at sites with vegetation classified as Types III, V, and VI (Table 5). Soils were a mixture of silt loams and fine sandy loams. Fifty-nine percent of soil profiles were classified as hydric; 88% had soil mottles and 35% had a surface organic layer. The pH ranged from 4.5 to 6.0 (Table 3).

As in Types I, II, and III, *Acer saccharinum* was dominant in the overstory of Type IV communities, but the understory of Type IV communities more closely resembled that of *A. rubrum* Alluvial swamp forests (Type V) and Alluvial terrace forests (Type VI). *Populus deltoides* and *A. rubrum* were both absent in the canopy of Type IV communities. *Quercus palustris* was a common associate in the Connecticut River basin, and *Betula nigra* in the Merrimack River basin. Type IV floodplain forest plots had a more substantial shrub layer than both Major-river (Types I and II) and Transitional (Type III) types, but less than both Types V and VI. The shrub layer of Type IV communities consisted mainly of *Cornus amomum* and *Cephalanthus occidentalis. Fraxinus pennsylvanica* saplings were present in most plots.

There was greater herbaceous diversity in Small-river floodplain forests than in floodplain forest Types I, II, and III. *Onoclea sensibilis* and *Boehmeria cylindrica* were most common, but associates included *Acer saccharinum* seedlings, *Cicuta maculata, Lysimachia terrestris, Sium suave,* and non-native taxa, such as *L. nummularia, Myosotis scorpioides, Rhamnus frangula,* and *Lythrum salicaria.* Four state-protected rare plant species were associated with this community type: *Mimulus alatus* (State Endangered), *Carex typhina* (State Threatened), *C. grayi* (State Threatened), and *Rumex verticillatus* (State Threatened; Kearsley 1999).

**Type V—Alluvial swamp forests (*Acer rubrum–A. saccharinum–Quercus bicolor* association).** Type V plots (15 plots at 6 sites) occurred along mainstem sections of smaller rivers in eastern Massachusetts (Assabet, Concord, Nashua, Shawsheen, and Threemile; Table 4). Plots classified as Type V were often associated at sites with plots classified as Types IV and VI (Table 5). This type appeared to be wetter and more seasonally inundated than the four *Acer saccharinum* dominated types (Types I–IV). Soils were typically silt loams; 67% had soil mottles and 67% had a surface organic layer. The pH ranged from 4.5 to 5.5 (Table 3).

Vegetation of plots classified as Type V was variable, as indicated by the lack of strong clustering in the DCA analysis (Figure 3). In general, the overstory of Type V plots was characterized by a mixture of *Acer saccharinum* and *A. rubrum* with lesser amounts of *Fraxinus pennsylvanica* and/or *Quercus bicolor.* Unlike Types I–IV, Type V communities had a well-developed shrub layer dominated by *Viburnum dentatum, Cornus amomum,* and the non-native plant *Rhamnus frangula.* As in Type IV communities, the herbaceous layer of Type V communities was characterized by a mixture of *Onoclea sensibilis* and *Boehmeria cylindrica*; however, the herbaceous layer differed in also having *Q. bicolor* seedlings, *Osmunda regalis,* and *Carex crinita.*

**Type VI—Alluvial terrace forests (*Acer rubrum–Carya ovata–Prunus serotina* association).** Type VI plots (14 plots at 5 sites) occupied upland ridges within Alluvial swamp forests (Type V) and high terraces above the active flood zone. Plots of this type occurred on the Nashua, Assabet, Blackstone, and Threemile Rivers and on high terraces in the Connecticut River basin (Table 4). Vegetation classified as Type VI was often associated with Types IV and V (Table 5). Type VI forests were river influenced and mesic, but they did not appear to experience regular flooding as indicated by the presence of a distinct soil organic layer. Soils were typically silt loams; 60% had soil mottles and 60% had a surface organic layer. The pH ranged from 4.5 to 6.0 (Table 3).

This community type showed the greatest within-group variability in plot composition, as indicated by the point spread in the DCA output (Figure 3). Although the plots were not highly clustered, they were well-differentiated from the other five floodplain forest community types. *Acer rubrum* was dominant in the canopy, and typically mixed with varying amounts of mesic hardwoods including *Carya ovata, Prunus serotina, Ulmus americana,* and *Tilia americana.* As in Type V communities, the shrub layer was well-developed, and *Viburnum dentatum* and *Ilex verticillata* were most common. The herbaceous layer was a species-rich mixture of *Onoclea sensibilis, Maianthemum canadense, Athyrium felix-femina, Osmunda cinnamomea,* and *Uvularia sessilifolia.*

## DISCUSSION

The greatest differences in vegetation composition and environmental characteristics among the floodplain forest community types occurred between Types I–III and Types IV–VI. These two groups were well-separated floristically, environmentally, and spatially. Types I–III occurred at sites on the Connecticut, Deerfield, and Housatonic Rivers, and Types IV and V occurred on small tributaries of the Connecticut River or on rivers in eastern

Massachusetts. Type VI occurred on elevated ridges and high terraces across the state, but more data are needed to clarify the distribution of and variation in high-terrace forests statewide.

Vegetation classified as Types I, II, and III often occurred together at a site. Sites with vegetation that was primarily classified as Type II had patches, usually on elevated sections, where *Matteuccia struthiopteris* was dominant (Type I), and depressions where *Boehmeria cylindrica* and *Onoclea sensibilis* were dominant (Type III). Similarly, sites with vegetation primarily classified as Type III had elevated sections dominated by *Laportea canadensis* (Type II). Overlap between community types within a single site also occurred among Types IV, V, and VI. Type IV forests in eastern Massachusetts had *Quercus bicolor* dominant (Type V) in low-lying, wet depressions and mesic, mixed-deciduous patches (Type VI) in elevated areas.

Although Types I–III and Types IV–VI were generally well-differentiated, overlap among defined community types did occur, particularly among Types III, IV, and V. These three types were all characterized by *Boehmeria cylindrica* and *Onoclea sensibilis* in the herbaceous layer, and differences in vegetation composition among the three types was subtle; however, differences in soil profiles and location supported the three types as recognizable associations.

Types I and II were also similar, and the differences observed in vegetation composition appeared to be primarily related to greater disturbance in areas classified as Type I. Riverine islands of the Connecticut and Deerfield Rivers where Type I vegetation assemblages were found had many canopy openings that were created by campers. Abandoned campsites were filling in with *Rhus typhina, Polygonum cuspidatum,* and a mixture of vines, including *Celastrus orbiculata* and *Vitis riparia.* The abundance of *Acer negundo,* which was associated with open, disturbed areas of Ohio floodplain forests (Hardin et al. 1989), was also indicative of greater disturbance in Type I forest plots.

**Comparison to other floodplain forest classifications.** Type I and II Major-river floodplain forests are similar in vegetation composition to floodplain forests of larger rivers in other New England states. Type I forests correspond to the *Acer negundo–Matteuccia struthiopteris* association described in Vermont, which occurs on sandy loams or open cobbles within the active floodplain of larger rivers. Type II forests correspond to Vermont's *A. saccharinum–M. struthiopteris* association, which occurs on coarse soils of levees of larger rivers (Sorenson et al. 1998). Elsewhere in New England a distinction between the two community types has not been made; however, Types I and II together correspond to the *A. saccharinum–M. struthiopteris–Laportea canadensis* association in New Hampshire (Bechtel and Sperduto 1998), the *A. saccharinum–Eupatorium rugosum* association in Connecticut (Metzler and Damman 1985), and to the *A. saccharinum* temporarily flooded forest alliance described for the eastern United States (Sneddon et al. 1998). Type I also contains elements of the *A. negundo* temporarily flooded forest alliance described for the Southeast which includes early successional vegetation of active floodplains and sandbars with a heavy vine component (Sneddon et al. 1998).

Type III *Acer saccharinum–Fraxinus pennsylvanica–Ulmus americana* floodplain forests correspond to *A. saccharinum/Onoclea sensibilis* floodplain forests described for Connecticut (Metzler and Damman 1985). Similar to Type III forests, *Matteuccia struthiopteris* was the dominant herbaceous taxon on the highest ridges within the community type in Connecticut (Metzler and Damman 1985). Type III forests are also closely affiliated with *A. saccharinum–O. sensibilis–Boehmeria cylindrica* communities occurring on silty soils of lower watersheds and lakeshores in Vermont (Sorenson et al. 1998) and *A. saccharinum–Carex crinita–O. sensibilis* associations in New Hampshire (Bechtel and Sperduto 1998). Type III forests correspond to the *A. saccharinum–U. americana–O. sensibilis* temporarily flooded forest community described for the Northeast (Sneddon et al. 1998).

Floodplain forest associations similar in composition to Types I, II, and III also occur on large rivers throughout the north-central United States. *Acer saccharinum* dominated forests have been described in detail in southeastern Wisconsin (Dunn and Stearns 1987; Menges 1986; Menges and Waller 1983), Ohio (Hardin et al. 1989; Hardin and Wistendahl 1983), northern Missouri (Dollar et al. 1992), New Jersey (Buell and Wistendahl 1955; Frye and Quinn 1979) and central Illinois (Brown and Peterson 1983; Peterson and Rolfe 1982). In all the forests described, *A. saccharinum* was mixed with *Fraxinus pennsylvanica* and *Ulmus americana* in the canopy, and *Laportea canadensis* was a major component of the understory.

Type IV forests are similar in vegetation composition and structure to *Quercus palustris–Fraxinus pennsylvanica* forests described in Connecticut (Metzler and Damman 1985), *Acer rubrum/Onoclea–Boehmeria* alluvial forests in Rhode Island (Barrett and Enser 1997), and *Q. palustris–A. rubrum–Carex grayi–Geum canadense* temporarily flooded forests described for New England (Sneddon et al. 1998). Type IV forests as described here differed from the above community types in having *A. saccharinum* rather than *A. rubrum* codominant with *Q. palustris* in the overstory.

Floodplain forest plots classified as Type V appeared to be seasonally saturated as indicated by prominent soil mottling close to the soil surface. Type V forests are similar in composition to *Acer rubrum–Onoclea sensibilis* forested wetlands found on poorly drained glacial lake sediments in Connecticut (Metzler and Tiner 1992) and to *A. rubrum* alluvial forests described for Massachusetts oxbows (Holland and Burk 1984). They correspond to the *A. rubrum–Fraxinus pennsylvanica* seasonally flooded forest alliance of low terraces and bottomlands occurring throughout the Eastern United States (Sneddon et al. 1998), and they are probably common in Massachusetts. *Acer rubrum* alluvial swamp forests similar to Type V forests have been described as a species-rich variant of *A. rubrum* swamps that are abundant throughout southern New England (Golet et al. 1993).

Type VI includes high floodplains that are flooded very infrequently, perhaps no more than several times per century (Jahns 1947). Type VI forests are similar in composition to high-terrace *Acer saccharum–Tilia americana–Matteuccia struthiopteris* forests in Vermont (Sorenson et al. 1998) and to high-terrace *A. saccharum–A. saccharinum–Fraxinus americana* forests in New Hampshire (Bechtel and Sperduto 1998), except that *A. saccharum* was uncommon in high-terrace plots in Massachusetts. Type VI forests are most closely related to *A. rubrum–Prunus serotina/Athyrium felix-femina* forests in New Hampshire which also had *Maianthemum canadense* and *Uvularia sessilifolia* as common associates (Bechtel and Sperduto 1998).

**Vegetation patterns in relation to environmental parameters.** The relationships between vegetation patterns and soil characteristics shown here are similar to those found across floodplain forest communities of the north-central United States. In New York, *Acer saccharinum–Fraxinus* sp. associations similar to Types III and IV occurred on fine-textured soils, while *Populus deltoides–Platanus occidentalis–Ulmus* sp. associations similar to Type I occurred on coarser-textured, alluvial sands and gravels (Huenneke 1982). In southern Illinois, Robertson and Weaver (1978) found that *Fraxinus pennsylvanica* attained its highest importance under prolonged and deep flooding, and occurred only at sites that had mottling near the surface. In Massachusetts, *F. pennsylvanica* attained its highest indicator values of 19 and 6 in community Types IV and V, respectively (Table 2). Results of the current study support the conclusions of Veneman and Tiner (1990) that *Boehmeria cylindrica* is restricted to hydric floodplain forest soils, while *Laportea canadensis* and *Matteuccia struthiopteris* are restricted to nonhydric soils. *Boehmeria cylindrica* was an indicator of floodplain forest community Types III, IV, and V, which occurred mainly on hydric silt loams. *Matteuccia struthiopteris* and *L. canadensis* were strong indicators of Type I and Type II, respectively, which both had predominantly coarse-textured, nonhydric soil profiles.

Soil pH was significantly different among floodplain forest community types in Massachusetts because there was a strong geographical distributional pattern among types, and soil pH appeared to be correlated with geographic location. Soils on the Connecticut, Deerfield, and Housatonic Rivers all had higher pH than those along rivers in eastern Massachusetts (Tables 3 and 4). That difference may be, in part, related to differences in flooding frequency among rivers. Dollar et al. (1992) found soil pH to be the closest correlate with variation in vegetation in northern Missouri floodplain forests and suggested that sites with higher flooding frequency and input of fresh alluvium had higher pH. This is supported in Massachusetts, where Types I, II, and III, which were located on large rivers with broad alluvial deposits (the Connecticut, Deerfield, and sections of the Housatonic Rivers), had the highest mean pH values. High pH values on the Housatonic River (pH 7–8) are also related to the influence of carbonate rich bedrock in western Massachusetts.

## CONSERVATION IMPLICATIONS

Thirty-eight natural or semi-natural true floodplain forest sites (Types I–IV) ranging in size from 1 to 30 ha were identified in Massachusetts: 20 were primarily Major-river floodplain forest communities (Types I and II), 6 were Transitional (Type III), and 12 were Small-river types (Type IV). Of the 38 sites identified, only 10 were found to be high-quality examples based on their condition, size, and landscape context. The ten high-quality floodplain forests included five Major-river sites (four on the Connecticut River and one on the Housatonic River), one Transitional site on the Mill River in Hatfield, and four Small-river sites (three in the Connecticut River basin and one on the Threemile River).

With the exception of the one site on the Housatonic River, all of the high-quality examples of Major-river floodplain forests occurred on either public land or privately owned conservation land. Transitional and Small-river floodplain forests are less well-protected in Massachusetts. Due to their limited occurrence in the state and the habitat that they provide for five state-protected rare plant species, Transitional and Small-river floodplain forest communities warrant active protection efforts.

Although land acquisition and conservation restrictions are important ways to protect the remaining examples of floodplain forests in Massachusetts, land protection alone probably will not maintain these sites as high-quality, natural floodplain forest communities. Non-native taxa were present at all floodplain forest sites surveyed, and they appeared to be most prevalent in areas where the canopy was open, the herbaceous layer was cleared, and the soil was disturbed. Non-native taxa appeared to be most abundant in eastern Massachusetts and on riverine islands and riverbanks of the Connecticut River that were heavily used by campers and boaters for recreation. Long-term vegetation studies will be needed to assess the spread of non-native taxa and the impact on floodplain forest community composition and structure.

The focus of the current study was on floodplain forests within the active zone of flooding. The two other alluvial forest types identified (Type V Alluvial swamp forests and Type VI High-terrace floodplain forests) require more information to determine their distribution, vegetation composition, environmental characteristics, and quality in Massachusetts. Type V Alluvial swamp forests are probably widespread, but high-quality examples may be limited. An in-depth inventory and classification of those communities is warranted with emphasis on identifying remaining high-quality examples.

Type VI High-terrace floodplain forests are very limited in Massachusetts because most river terraces have been cleared and converted to agriculture. Some high-terrace forests occur on the Millers, Westfield, and Green Rivers and parts of the Connecticut River, but more detailed inventories and vegetation and environmental analyses are warranted.

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# *JALTOMATA LOJAE* (SOLANACEAE): DESCRIPTION AND FLORAL BIOLOGY OF A NEW ANDEAN SPECIES

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ABSTRACT. *Jaltomata lojae* (Solanaceae) of southern Ecuador and northern Peru is described. This species is distinguished by the following features: finger hairs borne by the leaves and stems; a white, broadly infundibular to rotate corolla; exserted stigma; a broad nectary disk; and orange fruits. Corollas change from pale green to white at anthesis. Flowers are self-compatible, herkogamous, and sometimes protogynous. Microscopic, densely staining, multicellular glands that may be osmophores are located on the perianth. Berries are eaten by humans.

Key Words: edible fruit, floral biology, herkogamy, *Jaltomata,* osmophore, Solanaceae

*Jaltomata* includes about 40 neotropical herbaceous and shrubby species distributed from Arizona, U.S.A., to Bolivia, as well as on the Galápagos Islands and the Greater Antilles (Mione et al. 1993). The fruits of most species are eaten uncooked (Davis and Bye 1982; Mione 1992). This description of a new species is a contribution to ongoing systematic studies of this genus (Mione 1999; Mione and Bye 1996; Mione and Leiva 1997).

## MATERIALS AND METHODS

The description is based on the holotype and plants grown, from seed of the type collection, in the University of Connecticut (UConn) and Central Connecticut State University (CCSU) greenhouses. To look for structures that may release scent (osmophores), flowers were stained in 0.01% neutral red for several hours and then observed with bright field microscopy (Kearns and Inouye 1993). Observations on floral phenology were made in May of 1992 at UConn, and March to May of 1998 at CCSU. Chromosome counts were made with meiocytes of immature anthers stained with acetic carmine. Floral fragrance was evaluated by seven people who were blindfolded and asked to describe the fragrance of an empty jar and then a jar containing flowers. Jars were uncapped seconds before being placed in close proximity to the nose. To examine seed set, flowers were manually pollinated during the pistillate and hermaphroditic phases. Undehisced anthers were removed at the time of pollination.

## TAXONOMIC TREATMENT AND DISTRIBUTION

**Jaltomata lojae** Mione, *sp. nov.* TYPE: ECUADOR. Prov. Loja: by guard station on the E side of Celica, 1950 m, growing along roadside, 2 May 1991, *D. M. Spooner, R. Castillo, and L. López 5037* (HOLOTYPE: CONN). Figures 1 and 2.

A *J. cajamarca* Mione atque *J. sagasteguii* Mione foliis pilis dactyliformibus, corolla sub anthesi rotata et ovarii disco lato differt.

Perennial shrub; branches and leaves densely villous, bearing finger hairs, these sometimes gland-tipped, 0.15–6 mm long, becoming less villous with age. Leaves alternate, often geminate, ovate, to 15 cm long × 6 cm wide, the margin entire to sinuate-dentate, undulate, the petiole to 4.5 cm long. Inflorescence umbelliform, to 9-flowered. Peduncle 5–9 mm long (at flowering), pedicel 8–11 mm long (at flowering), both having a dense covering of erect finger hairs to 1.5 mm long, some hairs gland-tipped. Calyx (at flowering) light green, 9.5 mm in diameter, strongly reflexed, abaxially villous with gland-tipped finger hairs, forked hairs, and dendritic hairs all 1–2 mm long, and abaxially and adaxially with stalked multicellular glands 62–80 μm long (Figure 2), at fruit maturity calyx diameter to 12 mm. Corolla infundibular when partially open, rotate when fully open, white, with two green proximally positioned maculae straddling the radial vein to each corolla lobe (Figure 1), 5 prominent lobes alternating with 5 small lobules, 25–27 mm in diameter on plants we grew, 18 mm in diameter on the holotype, adaxially glabrous, abaxially with sparsely but evenly distributed stalked multicellular glands 62–80 μm long (Figure 2). Two classes of hairs extend out from the corolla margin: marginal hairs to 110 μm long, and submarginal (attached abaxially) hairs to 0.5 mm long. Stamens 5, 5 mm long; filaments on living plants angling away from style and slightly curved outward, villous on basal 1/4 of the length with unpigmented finger hairs to 1.2 mm long; anthers 2.1–2.5 mm long prior to dehiscing, 1.6–1.8 mm long after dehiscing, when corolla is fully open exserted out of corolla 2 mm,

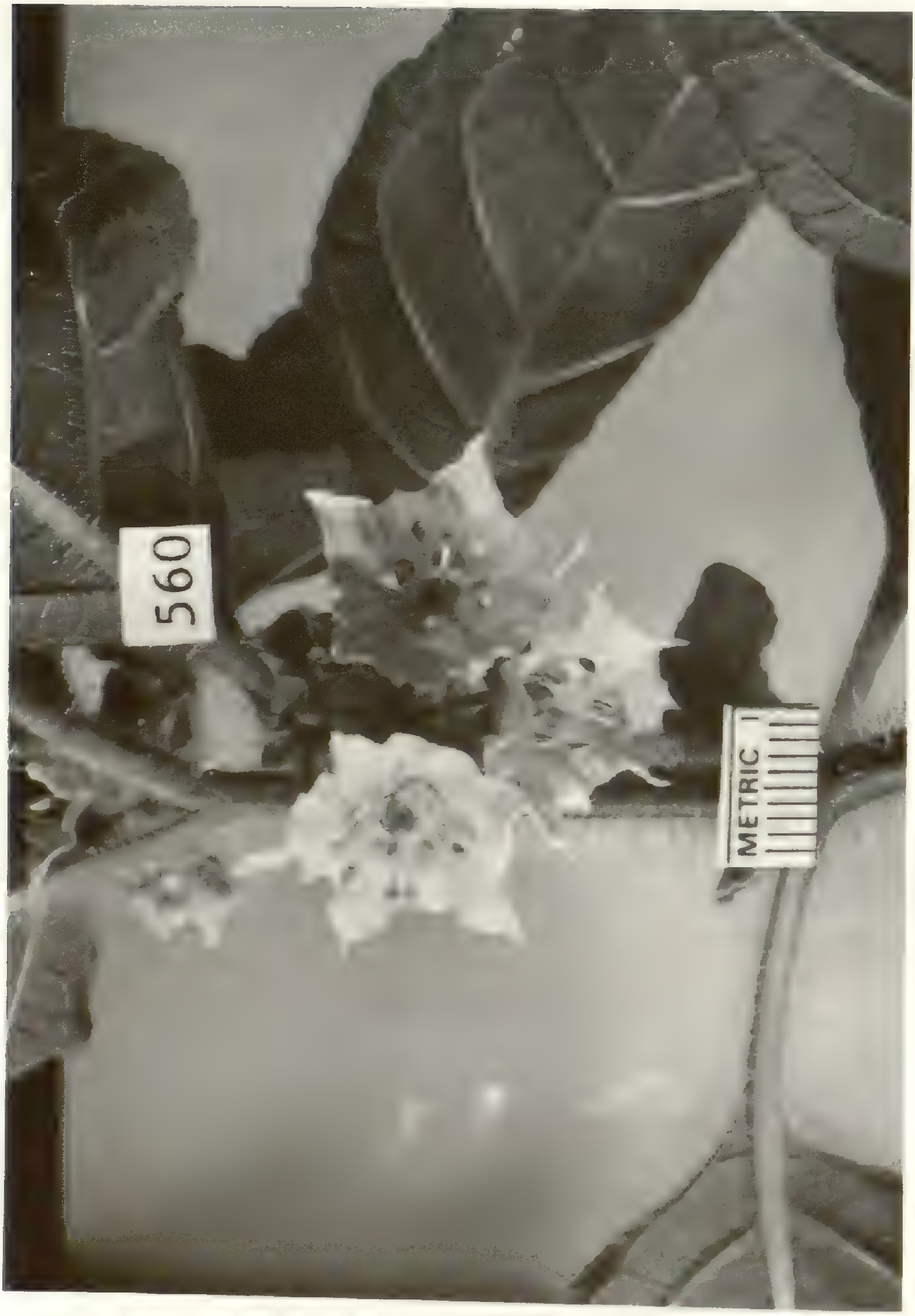

Figure 1. *Jaltomata lojae*. Inflorescence on plant grown from seed of the type collection. Units are millimeters.

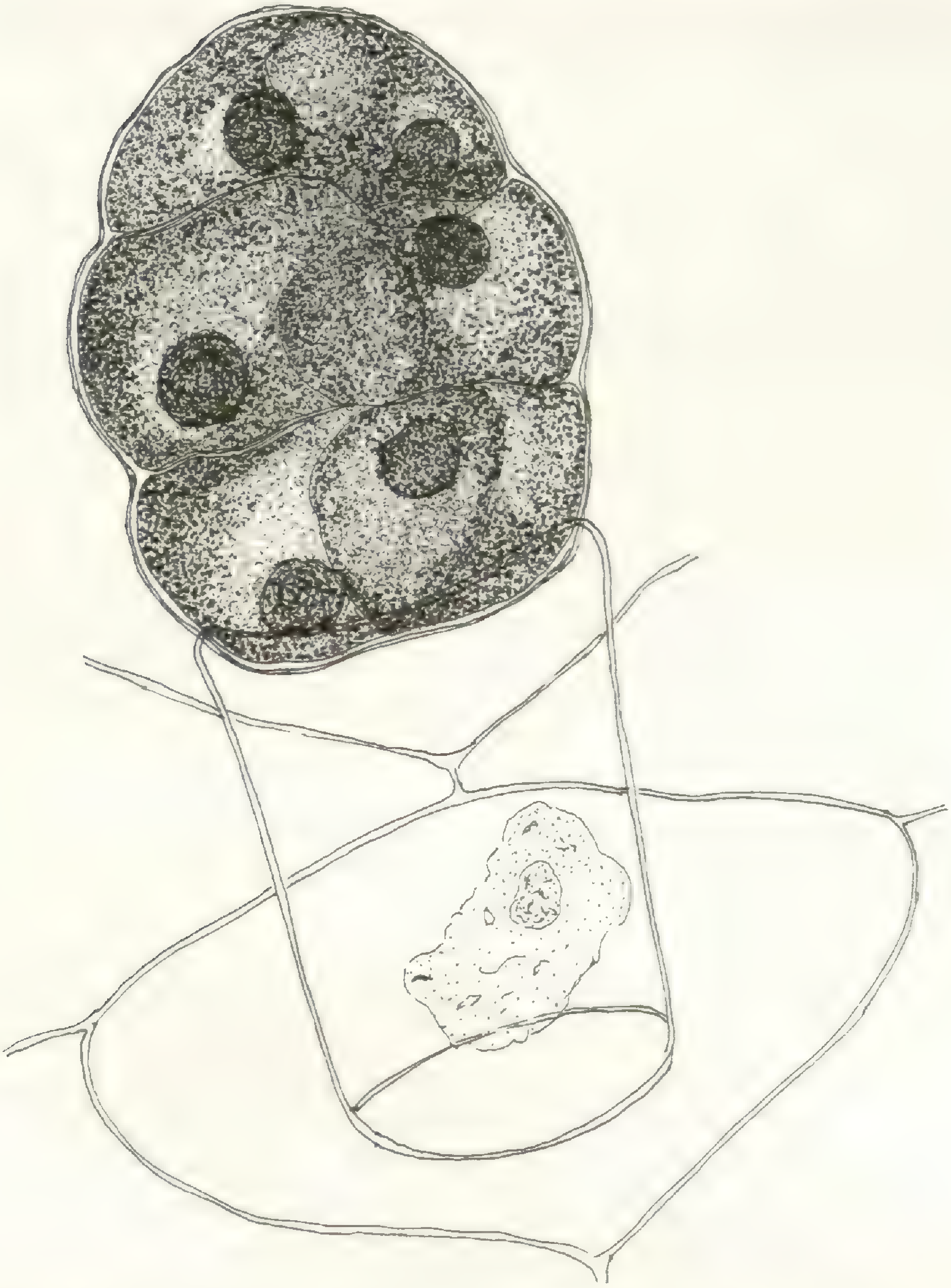

Figure 2. Perianth gland (75 μm long). Multicellular head stains deeply with neutral red, the stalk cell does not. Drawn by L. A. S. from plant grown from seed of the type collection.

otherwise included. Pollen grains 32.5 μm average diameter (n = 22 grains). Ovarian nectar disk orange (visible by eye on living flowers). Style 9–11 mm long, slender and straight (Figure 1), exserted 3–8 mm beyond the anthers; stigma shallowly bilobed, 0.4 to 0.75 mm wide on pressed specimens, broader than the style (Figure 1), the papillae 30–60 μm long. Mature fruits orange.

Seeds numerous, ovate to reniform, 1.3–1.6 mm long. Chromosome number $n = 12$ (nine counts).

DISTRIBUTION, ECOLOGY, LOCAL NAMES, USES. This species is distributed in southern Ecuador and northern Peru in disturbed habitats from 1900 to 2700 m elevation. Its local names are "ubillos" (*Ellemann 66799*) and "uvilla" (*van den Eynden and Cueva 342*). It has been used "for sunburn, used with alcohol for bath" (*Ellemann 66799*) and the fruits are edible (*van den Eynden and Cueva 342*).

OTHER SPECIMENS EXAMINED: specimens made from plants grown from seeds of the type collection *Mione 560* (CONN, HAO, MO, NY, QCA).

**Ecuador.** Prov. CHIMBORAZO: Cañon on the Río Chanchan, directly above the village of Huigra, 29–31 May 1945, *Camp E-3498* (NY); Prov. LOJA: Lugma Huycu 12 km north of Saraguro, 19 Jan 1989, *Ellemann 66799* (AAU not seen, NY); Cerro Sozoranga, Colaisaca-Utuana, km 0.5, 24 Apr 1994, *Jørgensen et al. 567* (MO not seen, NY); Sevillán, 26 Mar 1995, *van den Eynden and Cueva 342* (LOJA not seen, NY).

**Peru.** Dept. PIURA, Prov. Huancabamba: Abra de Porculla, entre Olmos y Jaén, ladera con monte bajo, 22 Apr 1964, *Ferreyra 15667* (K, US); Carretera entre Canchaque y Huancabamba, km del 16 al 25 desde Canchaque, 17 Apr 1987, *Díaz and Baldeón 2395* (MO, NY); Perculla, 2 May 1981, *Llatas and Laes 631* (HUT not seen, MO, NY).

## FLORAL BIOLOGY

To look for structures that may release scent, flowers were stained in dilute neutral red for several hours. The stigma (including papillae) stained darkly with neutral red but the style did not. Anthers and pollen stained darkly while filaments did not. Multicellular glands, located on the abaxial face of the corolla and both faces of the calyx, stained darkly, except for the stalk cell (Figure 2). Similar glands have been described on the leaves of *Solanum* (Seithe 1979) and *Physalis* (Seithe and Sullivan 1990). Neither the corolla margin hairs nor the hairs of the filaments absorbed stain. On the multicellular finger hairs only the glandular tip, when present, absorbed stain. Hand-sections of epidermal tissue of the ovary disk, stained and then observed with a compound microscope, revealed that the nectary disk absorbs stain only in the immediate vicinity of the stomata. The guard cells stained deeply, and the cells surrounding the guard cells also absorbed stain but staining was less intense. Flowers produced a subtle fragrance that was described as licorice-like, vanilla-like, or faintly sweet by the seven people polled and the authors. (Two of these people also detected a fragrance in the empty/control jar.)

Flowers remained open 5 to 7 days (mean 5.7 days, n = 9 flowers) and closed each night. Within an inflorescence one to four flowers were open at a time. The corolla was pale green prior to anthesis but after the corolla opened for the first time it became white and remained white. The anthers of a flower either dehisced a few at a time over the course of several hours, or two or three of the anthers dehisced one day and the others dehisced the next day. Anthers dehisced prior to 8:30 am. Some flowers exhibited one day of protogyny, with the stigma protruding through the partially open corolla. Two out of three flowers manually pollinated during the pistillate phase set seed, as did many (percentage not calculated) of the flowers that were manually pollinated during the hermaphroditic phase. In the greenhouse, plants did not set fruit unless hand-pollinated. This is likely due to herkogamy: the stigma is located 3 to 8 mm from the anthers. Nectar drops at the base of the corolla (alternating with the stamens) were large enough to be observed by eye. The broad, orange ovary disk is concentric around the green ovary and increases the diameter of the ovary by 1 to 1.5 mm over what the ovary diameter would be without the disk. Nectar seemed to be secreted by the ovarian disk but may also be secreted by the base of the corolla.

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# THE REPRODUCTIVE BIOLOGY OF *MAGNOLIA GRANDIFLORA*

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ABSTRACT. The reproductive biology of *Magnolia grandiflora* was investigated at three localities in south Louisiana. Over the 3–4 day flowering period, the flowers of *M. grandiflora* exhibited changes in sex expression (protogyny), stigmatic receptivity (self- and cross-compatibility to self-incompatibility), UV reflectance (strong reflectance of the stigmas to strong reflectance of the androphore), and pollinator reward (a hexose-dominated stigmatic nectar to pollen). Although beetles were occasional floral visitors and carried pollen, bees (non-native *Apis mellifera* and indigenous *Lasioglossum bruneri*) were frequent floral visitors and were the only floral visitors whose behavior showed any correlation with the array of floral changes that occurred over the 3–4 day flowering period.

Key Words: *Magnolia grandiflora,* reproductive biology, halictid bees, bees

*Magnolia* is considered to be primitive among angiosperms. A widely accepted view of the evolution of the flower is the Euanthial or Anthostrobilus theory. This hypothesis asserts that the primitive flower is large, actinomorphic, solitary, white (sometimes pink or yellow), and borne terminally. The primitive flower may have a showy, undifferentiated perianth and numerous floral parts arranged spirally on an elongated axis. The stamens are broad, three veined, and each has four elongate microsporangia on its adaxial surface. The gynoecium is apocarpous, with conduplicate carpels that enclose a few ovules (Arber and Parkin 1907; Bessey 1897, 1915; Canright 1952, 1960; Maneval 1914). This widely held view of the magnolian flower has been considered a theoretical starting point for understanding angiosperm evolution (e.g., Cronquist 1981). However, recent phylogenetic analyses (Crane 1985; Donoghue and Doyle 1989; Loconte and Stevenson 1990, 1991; Nixon et al. 1994), and fossil evidence of early angiosperms (Crane et al. 1994, 1995; Friis et al. 1994, 1995; Taylor and Hickey 1992) suggest that the morphological features of the archetypical angiosperm flower are unresolved.

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There is evidence to suggest that the diversification of angiosperms is associated with the diversification of the Apidae (Michener and Grimaldi 1988a, b; Crepet 1984, 1996; Crepet et al. 1991). The first occurrence of angiosperms, however, significantly predates the first occurrence of bees in the fossil record (Labandeira and Sepkoski 1993). The importance of the Diptera as early angiosperm pollinators has recently attracted attention (Kearns 1992; Kearns and Inouye 1993; Ren 1998). The Diptera have their origin in the Late Triassic–Early Jurassic (Rohdendorf 1974), prior to the origin and the diversification of angiosperms. Recent studies have shown that the floral foraging behavior of some groups of flies is similar to bees, and that certain groups of flies are faithful pollinators (Kearns 1992; Kearns and Inouye 1993; Ren 1998). Beetles are well known from the Mesozoic and occurred contemporaneously with the earliest known angiosperms. The large, unspecialized flowers of *Magnolia* are believed to be associated with the unspecialized "mess and soil" pollination syndrome of beetles (Faegri and van der Pijl 1979). Other investigators view beetle pollination in the Magnoliidae (Armstrong and Irvine 1990; Bernhardt and Thien 1987) and various other related groups (e.g. Cyclanthaceae; Beach 1982) as a specialized interaction involving floral modifications that are beneficial to the beetle pollinators. For example, in *Cyclanthus bipartitus* the bracts of the inflorescence produce a specialized high lipid tissue (50% by dry weight) that the beetles consume along with pollen (Beach 1982). Taxa that are unequivocally beetle pollinated frequently have floral modifications that specifically influence beetle behavior in the flower or inflorescence.

Despite a diversity of insect groups reported to visit *Magnolia,* most investigators have focused on the occurrence of beetles in the flowers of *Magnolia,* and on their role in pollen transfer (Baker and Hurd 1968; Delpino 1875; Dieringer and Espinosa 1994; Gibbs et al. 1977; Heiser 1962; Kikuzawa and Mizui 1990; Leppik 1975; Thien 1974). However, few of the floral features of *M. grandiflora* have been demonstrated to be specifically correlated with the floral behavior of the beetles.

The purposes of this study are as follows: a) to examine the floral characteristics that may function as insect attractants and/

or rewards, i.e., UV reflectance of floral parts, nectar secretion and composition, pollen availability, and the origin and longevity of the floral fragrance; b) to determine the self- and cross-compatibility of the flowers during anthesis and how this may relate to floral characteristics that are pollinator attractants and rewards; and c) to determine the kinds, numbers, and pollen loads of the various floral visitors, their behavior in the flowers of *Magnolia grandiflora,* and how this behavior may be related to floral characteristics that function as pollinator attractants and rewards.

## MATERIALS AND METHODS

The investigation was carried out at three localities in south Louisiana. Site #1 consisted of 59 cultivated trees located throughout the city of Lafayette, Louisiana, a suburban habitat. Site #2 was a single tree in the Louisiana State Arboretum, located in Evangeline Parish, Louisiana. The 121.41 hectare arboretum is a secondary growth forest that is 75–80 years old. The tree at Site #2 was used for observing pollinators in the forest canopy. Access to the 30–40 m forest canopy was achieved using mountain climbing techniques (Perry 1978). Site #3 consisted of a monoculture of over 30 trees of varying ages at the Louisiana Nursery, Opelousas, Louisiana. The nursery is located in a rural area and the trees were grown under horticultural conditions.

**Pollinator attractants and rewards.** To determine UV reflectance, flowers were photographed with a 35 mm camera using a Kodak Wratten UV Filter No. 18A. This filter transmits long wave UV radiation (320–400 nanometers). High speed (ASA 400) T-Max 400 professional black and white film was used to record the reflectance patterns.

The origin of the floral fragrance was determined by dividing the flower into separate parts (gynoecium, androphore, upper petals, and lower petals) and placing the separated floral organs in sterilized glass jars for 20 minutes. Thirty volunteers rated each of the floral parts according to the intensity of the odor (0 being the least and 5 being the most fragrant).

The flowers used for hand pollinations (see below) were monitored for the presence of a stigmatic exudate (nectar) over the four-day flowering period. The nectar used in the sugar analysis was collected from first-day flowers from a variety of plants at

Site #1 by using capillary tubes. (Nectar production ceased after the first day of anthesis.) The nectar was immediately placed in a cooler with ice packs, transported to the lab, and refrigerated at 1°C. The nectar was run on 20 × 20 cm EM Reagent, Silica Gel 60 Type plates. The gel thickness was 0.25 mm. After the plates were spotted, the sugars were run over 15 cm with one or two ascents, against ten sugar standards of various dilutions of a 15% (w/v) stock solution. The standards included glucose, mannose, fructose, galactose, xylose, ribose, rhamnose, sucrose, maltose, and mannitol. The solvent used was a 9:6:3:1 solution of n-butanol : acetic acid : chloroform : water. The plates were developed at 100–110°C for 10–20 minutes after being sprayed with a 1:3 (v/v) solution of sulfuric acid : methanol. The presence or absence of protein in the nectar was determined by the application of 2% ninhydrin in acetone (w/v) to nectars spotted on a Thin Layer Chromotography (TLC) plate and then baked at 100°C.

The mean number of pollen grains per flower was estimated by removing thirty stamens from three flowers collected from three different trees at Site #1. Each of the thirty stamens was agitated with 0.01% Tween 20 in a known volume of water. Pollen grains were counted on a hemacytometer grid. The mean number of pollen grains per stamen and flower was calculated. In addition, the number of ovules per flower was recorded to derive an estimate of the pollen-ovule ratio (P/O).

**Determination of self- and cross-compatibility.** At Site #1, flowers were hand pollinated to determine stigmatic receptivity and cross- and self-compatibility. The pollinations were divided among ten treatments, 14–39 plants per treatment. Four of the treatments consisted of cross-pollinations on days 1–4 of anthesis, four consisted of self-pollinations on days 1–4, one treatment was an unpollinated bagged control for days 1–4, and one treatment was an unbagged control for days 1–4, to determine the seed set under natural conditions.

Prior to anthesis, the gynoecia of the hand pollinated flowers were bagged with tubular nylon hosiery. After the hand pollinations, the flowers were tagged. Pollen was collected for various pollinations in paper envelopes. The pollen was stored at −10°C with a desiccator (Williams 1980). To insure that all pollinations from the stored pollen had a similar level of viability, the duration of pollen viability was tested. Flowers were collected from three different trees during the first morning of anthesis, the petals were removed, and the floral column with the stamens was placed on a sheet of paper. Within 24 hr., the anthers dehisced, the floral column was removed, one aliquot of pollen was stored at room temperature (21°C), and one aliquot was stored at −10°C. Pollen viability was tested from each of the aliquots daily for five consecutive days following anthesis using the method of Alexander (1969).

The gynoecia were collected as they ripened and the number of stigmas, the number of carpels setting seed, and the number setting two seeds were recorded. The percentage of ovules fertilized was calculated by dividing the total seed set by the total number of ovules (2/carpel) and multiplying by 100. The percentage of ovules fertilized for the ten treatments was compared using ANOVA (analysis of variance). A general linear model for unbalanced designs was chosen and a two-factor general linear model ANOVA was run on Minitab (Cruze and Weldon 1989). The model was fitted with two main effects, crossed and selfed treatments. The four days over which pollinations were made were treated as an interactive factor with four levels. F-ratios were compared at the 0.01 level of significance to detect differences among treatments. Significant differences between treatments were then tested using Tukey's multiple-comparison (W) procedure with Alpha = 0.05 (Cruze and Weldon 1989; Ott 1988).

**Observations of insects.** The types of insects and the number of visits by each taxon at Sites #1, #2, and #3 were recorded by direct observation or by videotape. Each of the three sites was monitored 14 times at equally spaced intervals between May 19 and July 29. Insect visitor data were recorded for an average of three hours per observation time, yielding a total of 42 hours of observations per site. Unfamiliar insects were collected for identification and five individuals of each species were collected as voucher specimens. All insects except thysanopterans were placed in a kill jar containing ethyl acetate. Thysanopterans were fixed in alcohol-glycerine-acetic acid (AGA) killing solution. After two weeks in the AGA, the thysanopterans were dehydrated in an alcohol series and mounted on microscope slides for identification (Borror et al. 1989). For each site the number of visits by each type of insect was recorded. The duration of the visits was recorded by direct observation and from time lapse and real-time videotaping of the flowers. The pollen load per individual of each insect species was calculated as the mean number of grains carried on the insect specimens collected. The pollen carried on the corbicula of *Apis mellifera* was not available for stigmatic deposition and so was not included in the pollen load of this species. However, the pollen carried on the legs of halictid bees dislodged easily and was available for stigmatic deposition; thus these pollen grains were included in the pollen load for this species.

The relative importance (RI) of various insect species as pollinators was calculated using the following equation:

$$RI_i = \frac{P_i \times V_i}{(P \times V)} \times 100$$

where

$RI_i$ = Index of relative importance of pollinator i,

$P_i$ = Mean pollen load of pollinator i,

$P$ = Sum of mean pollen loads of all insects,

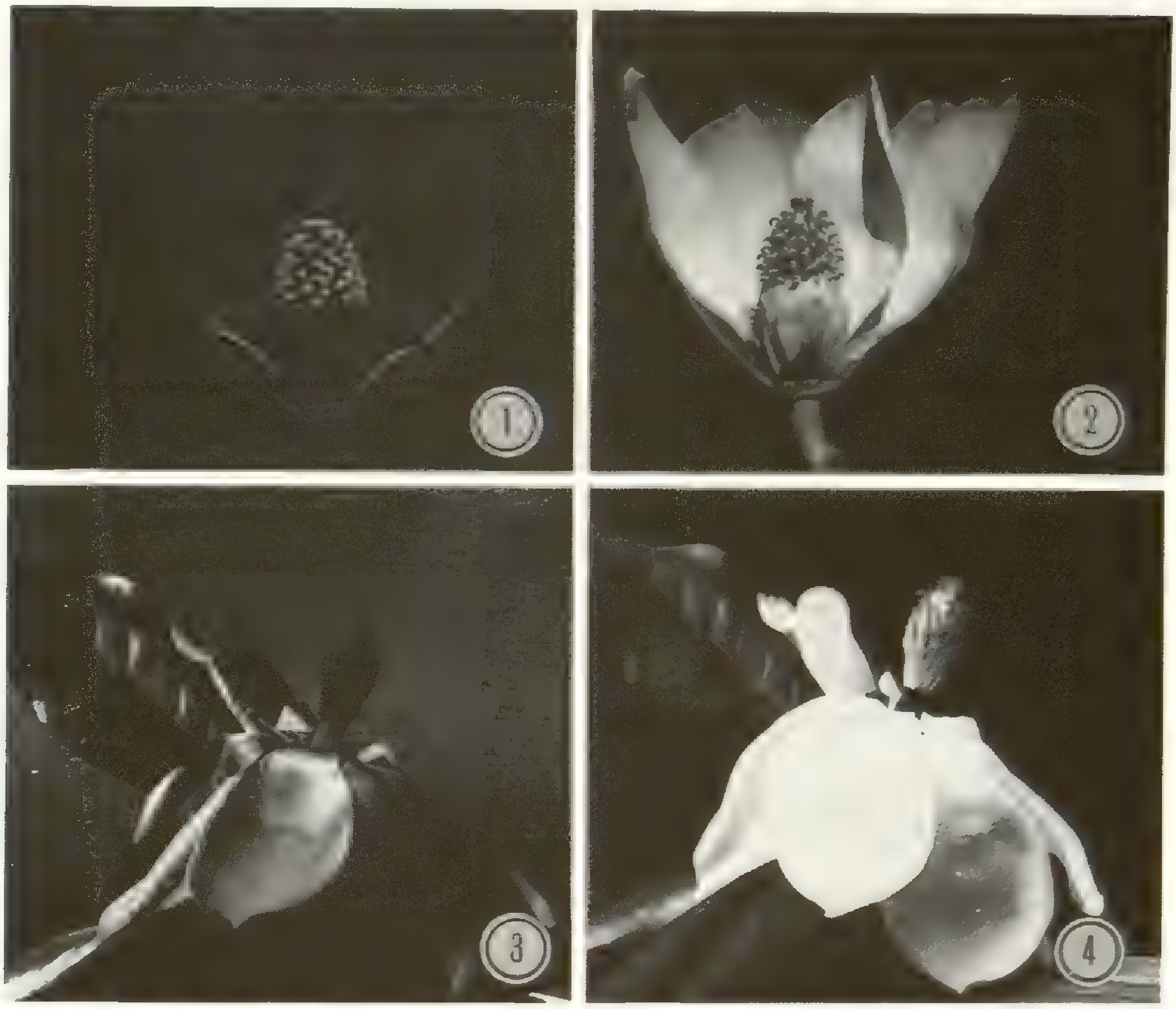
$V_i$ = Number of visits of pollinator i,

$V$ = Total number of insect visits.

Overall or total RI was calculated for each taxon by using the mean pollen load of the taxon over all three sites and the mean number of visits by that taxon at all three sites. A correlation coefficient was run on Minitab for all comparisons of insects recorded at the three sites.

## RESULTS

**Pollinator attractants and rewards.** On the first day of anthesis the stigmas strongly reflected UV light (Figure 1, 2). On the second day of anthesis the stigmatic reflectance was evident, but had significantly faded in comparison to the first day of anthesis (Figure 3). By the third day of anthesis the UV reflectance of the stigmas was no longer evident. As the stigmatic reflectance faded on the second day of anthesis, the androphore, from which the stamens had abscised, reflected UV light in a checkered pattern (Figure 3, 4). The reflectance of the androphore was evident on the third day of anthesis, but was not detectable on the fourth



Figures 1–4. The two stages in *Magnolia grandiflora* floral phenology. 1. Ultraviolet photograph of a first day flower showing the reflective stigmatic crests. 2. Photograph of a first day flower taken without the UV filter. 3. Ultraviolet photograph of a second day flower showing the faded stigmas and "checkered pattern" of the reflective androphore (arrowhead). 4. Photograph of a second day flower without the UV filter.

day of anthesis. Throughout the four days of anthesis the corolla strongly absorbed UV light.

In the determination of the origin of the floral fragrance, 29 of the 30 volunteers rated the petals most fragrant, and the androphore least fragrant.

Nectar secretion associated with the stigmas occurred only on the first day of anthesis. Nectar was not evident on days 2–4. Using thin layer chromotography (TLC), three sugars were identified in the stigmatic exudate collected soon after the flowers opened on the first day of anthesis; these were glucose, fructose, and sucrose. Glucose and fructose, when visualized on the TLC plates, showed a similar intensity to the 15% (w/v) standard sugar solutions. Sucrose, although easily detectable, consistently exhibited less intensity, suggesting that lesser amounts of sucrose were present in the stigmatic nectar than glucose and fructose. Nectar collected 3–6 hr. after anthesis had no detectable sucrose, indicating that as the nectar ages, the sucrose breaks down into hexose sugars. Nectars are known to contain protein (Baker and Baker 1975, 1983) and the nectar of *Magnolia grandiflora* tested positive for protein.

On the second day of anthesis the stamens dehisced and subsequently abscised from the androphore, falling into the cup-shaped petals. It was in the cup-shaped petals that magnolia pollen was available in abundance. The estimated mean number of pollen grains per flower was 58,000,000. The pollen-ovule ratio was estimated to range from 207,000:1 to 520,000:1 with an average of 412,000:1.

**Self- and cross-compatibility.** To insure that differences in seed set were not due to differences in pollen viability from day to day, pollen was tested for viability. On the day of anther dehiscence (day 2 of anthesis) a mean of 94.5% of the pollen grains were viable. There was no significant decrease in pollen viability for the five consecutive days following anthesis when pollen was stored at 21°C or −10°C.

Results of the hand pollinations showed that on the first day of anthesis the stigmas were receptive to geitonogamous and xenogamous pollinations. On the first day of anthesis the average seed set for xenogamous pollinations was 55%. The average seed set for geitonogamous pollinations was 38%, which was significantly lower than the cross-pollinated flowers (Table 1). On the second day of anthesis cross-pollinated flowers averaged 27% seed set, on the third day 13% seed set, and on the fourth day 2% seed set, which was not significantly different from the bagged, unpollinated control (Table 1). This indicates that receptivity to xenogamous pollinations was gradually reduced over the 3–4 day flowering period. In flowers that were self-pollinated, there was a significant decrease in percent seed set during the second day of anthesis, i.e., from 38% on the first day, to 5% on the second and third day of anthesis, and 3% on the fourth day of anthesis (Table 1). Seed set on days 2, 3, and 4 in the self-pollinated flowers was not significantly different from the unpollinated, bagged control. The unbagged, untreated control aver-

Table 1. Mean seed set resulting from hand pollinations of *Magnolia grandiflora* flowers. Cells with different bold letters **a**, **b**, **c**, **d** are statistically different at Alpha = 0.05. n = number of flowers/treatment; $\bar{x}$ = mean % seed set for each treatment; sd = standard deviation.

| Treatments | Day 1 | Day 2 | Day 3 | Day 4 |
|---|---|---|---|---|
| Cross | n = 14<br>$\bar{x}$ = 55 **a**<br>sd = 24 | n = 16<br>$\bar{x}$ = 27 **b**<br>sd = 20 | n = 18<br>$\bar{x}$ = 13 **c**<br>sd = 17 | n = 14<br>$\bar{x}$ = 2 **d**<br>sd = 3 |
| Self | n = 20<br>$\bar{x}$ = 38 **b**<br>sd = 24 | n = 20<br>$\bar{x}$ = 5 **d**<br>sd = 11 | n = 12<br>$\bar{x}$ = 5 **d**<br>sd = 15 | n = 15<br>$\bar{x}$ = 3 **d**<br>sd = 4 |
| Control (bagged, unpollinated) | n = 39<br>$\bar{x}$ = 5 **d**<br>sd = 11 | | | |
| Control (unbagged, untreated) | n = 20<br>$\bar{x}$ = 34 **c**<br>sd = 26 | | | |

aged 34% seed set, which is assumed to approximate seed set under natural conditions.

The results of the hand pollinations in the cross-pollinated flowers showed that from day 1 to day 4 there was a stepwise reduction in receptivity. Each day was significantly less receptive than the previous day, culminating on day 4, which was not significantly different from the unpollinated, bagged control. The flowers were self-compatible on the first day of anthesis and seed set in the self-pollinated flowers was similar to the percent seed set in the unbagged, untreated control. However, on the second, third, and fourth days of anthesis, self-pollinated seed set was not significantly different from the unpollinated, bagged control, indicating that the flower was essentially self-incompatible after the first day of anthesis.

**Observations of insects.** Seven orders of insects accounted for more than 99% of the insect visits to *Magnolia* flowers at all three sites. The correlation coefficient for all comparisons of the insects recorded at the three sites was greater than 0.93, indicating that the types of insects at each site, and the relative proportions of the insects visiting *Magnolia* at each site were similar. Frequencies of visits by the various insects varied among the sites, with Site #2 having almost twice as many insect visitors as Sites #1 and #3 over a similar time interval.

Hymenoptera and Thysanoptera accounted for 87% of the insect visits and Coleoptera, Diptera, Hemiptera, Homoptera, and Plecoptera for the remaining 13% of total insect visits (Table 2). Despite the occurrence of seven orders of insects visiting *Magnolia* flowers, Hymenoptera carried 98.9% of the pollen (excluding the pollen found in the corbiculae). The other six orders accounted for only 1.0% of the pollen carried (Table 3). The relative importance (RI) of each of the insect groups as pollen carriers shows the Hymenoptera with an RI of 99.98 over all three localities (Table 4). If the non-native honeybee (*Apis mellifera*) and the recently introduced *Magnolia* beetle (*Odontopus calceatus*) are excluded from the calculation, native halictid bees have an RI of 94.77 over all three localities (Table 5).

The Hymenoptera were the most frequent visitors of *Magnolia grandiflora* and carried the most pollen (Table 2, 3). Two species of ants belonging to the Formicidae accounted for 35 visits. The most common of these two ant species carried no pollen. The

Table 2. Number of insects per family visiting *Magnolia grandiflora* at each site, and combined over all sites. The number of visits per taxon are for the total 42 hr. of observations at each site. [1]Combined visits over all sites as a % of the total number of insect visits for all taxa.

| Insect Taxon | Number of Insect Visits | | | | % |
|---|---|---|---|---|---|
| | Site #1 | Site #2 | Site #3 | Combined | of Total[1] |
| HYMENOPTERA | | | | | |
| Apidae | 433 | 1,049 | 560 | 2,042 | 70.7 |
| Halictidae | 19 | 38 | 1 | 58 | 2.0 |
| Other | 36 | 8 | 0 | 44 | 1.5 |
| TOTAL | 488 | 1,095 | 561 | 2,144 | 74.2 |
| COLEOPTERA | | | | | |
| Cantharidae | 2 | 29 | 7 | 38 | 1.3 |
| Curculionidae | 90 | 0 | 62 | 152 | 5.3 |
| Dermestidae | 0 | 29 | 0 | 29 | 1.0 |
| Mordellidae | 41 | 32 | 3 | 76 | 2.6 |
| Other | 1 | 7 | 10 | 18 | 0.6 |
| TOTAL | 134 | 97 | 82 | 313 | 10.8 |
| THYSANOPTERA | | | | | |
| Thripidae | 166 | 198 | 3 | 367 | 12.9 |
| ALL OTHER ORDERS | 27 | 25 | 12 | 64 | 2.2 |

other species had an average pollen load of 2.75 grains each. At Site #1 five cuckoo bees (Apidae, Tribe Epeolini; absent from Sites #2 and #3) were collected, but no pollen was present. Two carpenter bees (*Xylocopa virginica*) visited flowers in the forest canopy at Site #2 and a single carpenter bee was observed at Site #1, and had a pollen load of 1350 pollen grains. The honey bee (*Apis mellifera*) dominated the floral fauna with an estimated 2042 visits out of 2888 recorded insect visits over the course of the field study. As many as ten honey bees were in a single flower at a time. Honey bees were most active in late morning to early afternoon. Honeybees averaged about 34 visits/hour as determined from videotaped flowers at Sites #2 and #3. The mean pollen load of *A. mellifera* (excluding the corbiculae) was estimated to be 22,200 pollen grains each (n = 4). The corbiculae were estimated to hold 73,000 pollen grains each (n = 4). A single species of solitary bee of the Andrenidae was collected six times at Site #2 and was found to carry a mean pollen load of 8300 pollen grains (n = 3). Andrenid bees were absent from Sites

Table 3. Statistical description of *Magnolia* pollen grains carried per insect. Taxa with less than 0.01% of total are excluded. [1]Standard error. [2]Percent of the total mean pollen load of all taxa combined. [3]Excluding pollen contained in the corbiculae. *No standard error due to sample size.

| Insect Taxon | n | Mean | SE[1] | % of Total[2] |
|---|---|---|---|---|
| HYMENOPTERA | | | | |
| *Andrena vicina* | 3 | 8,333 | 1,816.30 | 17.10 |
| *Apis mellifera*[3] | 4 | 22,200 | 7,598 | 45.60 |
| *Lasioglossum bruneri* | 3 | 16,250 | 2,602.10 | 33.40 |
| Unidentified Formicidae | 4 | 3 | 1.60 | 0.01 |
| *Xylocopa* | 1 | 1,351 | * | 2.78 |
| COLEOPTERA | | | | |
| Cantharidae | 5 | 97 | 39.30 | 0.20 |
| Chrysomelidae | 3 | 265 | 228.60 | 0.60 |
| Curculionidae | 5 | 26 | 10 | 0.05 |
| Dermestidae | 5 | 8 | 2.40 | 0.02 |
| Mordellidae | 5 | 23 | 7.60 | 0.05 |
| Unidentified | 3 | 7 | 7.30 | 0.02 |
| DIPTERA | | | | |
| Unidentified | 10 | 2 | 1.20 | 0.01 |
| HEMIPTERA | | | | |
| Pyrrhocoridae | 1 | 64 | * | 0.10 |
| HOMOPTERA | | | | |
| Cicadellidae | 3 | 8 | 1.80 | 0.02 |

#1 and #3. The solitary halictid bee, *Lasioglossum bruneri,* was present at all three sites, with 19 individuals collected at Site #1, 38 at Site #2, and 1 at Site #3. These bees carried a mean pollen load of 16,300 grains (n = 3; excluding the corbiculae). A corbicula was found to carry approximately 44,300 grains (n = 1).

Thysanopterans were present at all three sites. At Site #1, 20.4% and at Site #2, 13.9% of all insects collected were thrips. Initially thrips were not noticed at Site #3, however thrips were later collected from preserved flowers. The Thysanoptera were too numerous and small to count in the field and were collected from preserved flowers at the end of the field season. The number of thrips does not represent the abundance of these insects over the entire study period. The 400–500 μm thrips collected from day 1 flowers (female phase) had pollen grains adhering to their bodies, suggesting that thrips do transfer pollen from flower to

Table 4. Relative importance (RI) of pollinators by family (calculated using all insects). Families with an overall pollinator RI less than 0.01 are excluded.

| Insect Taxon | Relative Importance of Pollinators | | | |
|---|---|---|---|---|
| | Site #1 | Site #2 | Site #3 | Overall |
| HYMENOPTERA | | | | |
| Apidae | 97.7 | 98.01 | 99.87 | 98.45 |
| Andrenidae | 0 | 0.11 | 0 | 0.06 |
| Halictidae | 2.28 | 1.87 | 0.09 | 1.47 |
| COLEOPTERA | | | | |
| Chrysomelidae | 0.01 | 0.01 | 0.04 | 0.02 |

flower. Despite their high abundance, thrips carried an average of 0.3 pollen grains each.

The highest number and relative abundance of coleopterans was found at Site #1 on cultivated trees in the suburban habitat. One of the most common beetles was the recently introduced magnolia beetle, *Odontopus calceatus.* This species was also re-

Table 5. Relative importance (RI) of pollinators by family (calculated with *Apis mellifera* and *Odontopus calceatus* excluded). Families with an overall RI less than 0.01 are excluded.

| Insect Taxon | Relative Importance of Pollinators | | | |
|---|---|---|---|---|
| | Site #1 | Site #2 | Site #3 | Overall |
| HYMENOPTERA | | | | |
| Andrenidae | 0 | 5.36 | 0 | 3.55 |
| Halictidae | 98.98 | 93.66 | 69.74 | 94.77 |
| *Xylocopa* | 0.15 | 0.14 | 0 | 0.14 |
| COLEOPTERA | | | | |
| Cantharidae | 0.01 | 0.06 | 0.39 | 0.05 |
| Chrysomelidae | 0.55 | 0.52 | 29.41 | 1.21 |
| Dermestidae | 0 | 0.06 | 0 | 0.04 |
| Mordellidae | 0.27 | 0.15 | 0.40 | 0.19 |
| DIPTERA | | | | |
| Diptera/Other | 0 | 0.01 | 0.01 | 0.01 |
| HEMIPTERA | | | | |
| Pyrrhocoridae | 0 | 0.03 | 0 | 0.02 |
| THYSANOPTERA | | | | |
| Thripidae | 0.02 | 0.01 | 0.01 | 0.02 |

corded from Site #3, but was absent from the forest canopy (Site #2). Magnolia beetles carried a mean pollen load of 26 grains (n = 5). One species of Cantharidae was common at Site #2 and carried the largest pollen load (an average of 97 grains, with a maximum of 203 grains) of all the coleopterans collected. Members of the Mordellidae occurred at all sites and were common at Sites #1 and #2. A total of 41 individuals were collected at Site #1, and 32 individuals at Site #2. Members of the Dermestidae were collected at Site #2 and had an average pollen load of 8 grains. Beetles represented by a single individual were not identified. Coleopterans were observed to remain in flowers for long periods of time, and many remained in the flower for the entire time the flower was observed (up to 24 hr.). The random examination of over 400 flowers on the first day of anthesis (female phase) resulted in the observation of two beetles, one member of the Cantharidae and one of the Lampyridae.

Dipterans were present at all sites although no one species was most common. Dipterans were most abundant at Site #1 where 16 of 25 dipterans collected were *Plecia nearctica* (Bibionidae). Other dipterans collected included three species of the Asilidae and four unidentified taxa at Site #1. At Site #2 three species of the Sciomyzidae and three unidentified species were collected. In addition 16 other taxa were observed, but were not captured for identification. Dipterans at Site #3 included two members of the Phoridae, six species of the Bibionidae, and one unidentified species. Of the dipterans collected, most carried no pollen and three species carried five, seven, and eight grains, respectively.

Of the remaining insects collected, one plecopteran of the Perlidae was collected at Site #3, but carried no pollen. Four homopterans, all members of the Cicadellidae, were collected and carried an average of 8 pollen grains/insect. Two species of hemipterans were collected; *Nezara viridula* was collected at Sites #2 and #3 and carried no pollen, and *Euryophthalmus succinctus* was collected from Site #2 and was carrying 64 pollen grains.

## DISCUSSION

The flowers of *Magnolia grandiflora* exhibited interactions among floral movements, pollinator attractants and rewards, and stigmatic receptivity. On the first day of anthesis the flowers opened early in the morning presenting the receptive stigmas (female phase). Concomitant with anthesis was a conspicuous stigmatic nectar and a strong floral fragrance, which emanated from the petals. Three sugars were identified in the stigmatic exudate. Fresh nectar (nectar collected during the early morning) was comprised of glucose and fructose with a lesser amount of sucrose (i.e., a hexose-dominated nectar; Baker and Baker 1975). Baker and Baker (1975, 1983) have shown that hexose-dominated nectars also contain measurable amounts of protein. The stigmatic nectar of *M. grandiflora* tested positive for protein. Nectar that had been exposed to air temperature for 3–6 hr. was comprised of only glucose and fructose; the sucrose became undetectable using thin layer chromotography. This suggests that the sucrose may have been enzymatically broken down into hexose sugars as the nectar aged. Baker and Baker (1975, 1983) have demonstrated that hexose-dominated nectars are usually associated with the dish-bowl flower morphology, and pollination by short-tongued bees (e.g., honeybees and halictid bees) or flies. The reflectance of UV light was particularly strong by the stigmas (Figure 1, 2). The highly reflective stigmas occurred against a corolla that strongly absorbed UV light (Figure 1, 2). The floral fragrance and the highly reflective stigmas in combination with the hexose-dominated stigmatic nectar are floral attractants that can potentially direct pollinators to the receptive stigmas in first-day flowers. First-day stigmas were receptive to geitonogamous and xenogamous pollinations (Table 1). Based on our field observations and videotape of floral visitors at all three sites during the first day of anthesis, 88% of the honeybee (n = 366) and 96% of the halictid bee (n = 23) landings were on the stigmas. The bees spent an average of 1 minute 14 seconds (n = 44) in first-day flowers. We interpret this bee behavior as a response to olfactory (floral fragrance) and visual (UV reflectance of the stigmas) floral cues that are associated with nectar as the reward. After 1500 hours on the first day of anthesis the flowers began to close, were fully closed by 1900–2000 hours, and remained closed until the early morning of the second day of anthesis.

On the second day of anthesis the flowers re-opened early in the morning. At this time the anthers dehisced and then abscised from the androphore throughout the day, falling into the cup-shaped petals. The flowers remained open continuously for the next 2–3 days. The floral fragrance remained detectable. The UV reflectance of the stigmas had faded but was still detectable (compare Figure 1 with Figure 3), however, the reddish-purple androphore strongly reflected UV light in a checkered pattern after all of the stamens had abscised (Figure 3, 4), i.e., the conspicuous UV reflectance had shifted from the stigmas to the androphore. The stigmatic nectar was no longer evident, however, pollen was now available in abundance. The estimate of the mean number of pollen grains per flower was approximately 58,000,000. It appears that the pollinator reward had also shifted from nectar to pollen (Yasukawa et al. 1992). The pollen/ovule ratio (P/O) was calculated for three flowers from three different trees. The P/O averaged 412,000:1. The high P/O is not consistent with the occurrence of constant pollinators and suggests pollen limitation (Cruden 1977; Cruden and Miller-Ward 1983). However, in *Magnolia* the pollen was not presented while the stamens were attached to the androphore, but on the cup-shaped petals after they had abscised. There was frequent loss of pollen-laden stamens due to disturbance of the flowers (e.g. by wind). The high P/O may compensate for the losses due to this unusual type of pollen presentation. Stigmatic receptivity remained high for cross-pollination, however, self-compatibility was greatly reduced (Table 1). There was no significant difference in seed set between the bagged unpollinated control and the self-pollinated flowers on the second day of anthesis. Seed set in cross-pollinated ovules was lower than cross-pollinated ovules on the first day, but was significantly higher than the self-pollinated ovules on the second day of anthesis (Table 1). The shift in pollinator attractants and reward on the second day suggests that a concomitant shift in pollinator behavior in the flower should also occur. Based on our observation and videotape of pollinators at all three sites on the second day of anthesis, 62% of the honeybee (n = 282) and 71% of the halictid bee (n = 7) landings were on the reddish-purple androphore, the bees then made a 180° turn and began to forage for pollen on the abscised stamens held in the cup-shaped petals. Once in the cup-shaped petals, the bees often held the stamens like lollipops, using their forelimbs to scrape pollen from the anthers. Honeybees spent an average of 2 minutes 52 seconds (n = 50) in second-day flowers. Thus, the shift in the visual cue for pollinators (UV reflectance of the stigmas to reflectance of the androphore) and the shift in the pollinator reward (from nectar to pollen) correlated with changes in the foraging behavior of bees in the flowers from the first to the second day of anthesis.

On the third day of anthesis floral fragrance was still evident, but had faded dramatically and the stigmas no longer reflected UV light. The flower was still cross-compatible (Table 1), however receptivity was reduced further, though it was still significantly higher than the bagged, unpollinated control. The behavior of the hymenopteran floral visitors was similar to the behavior observed in second-day flowers.

On the fourth day of anthesis floral fragrance and UV reflectance were no longer evident and the flower was no longer receptive. In addition, a majority of the stamens (and hence the pollen) had been lost from the wilting, cup-shaped petals. The number of hymenopteran visits also dropped off dramatically.

In our observations at all three sites (including videotape taken at Sites #2 and #3), hymenopterans were the only floral visitors whose behavior showed any correlation with the array of floral changes that occurred over the 4-day period in the flowers of *Magnolia grandiflora.* It is expected from our investigation of floral movements, stigmatic receptivity, and the pollinator attractants and rewards, that hymenopterans play an important role in the pollination of *Magnolia.*

Based on our observation of floral visitors at all three sites, the most frequent visitors of *Magnolia grandiflora* were hymenopterans (bees; Table 2). Coleopterans are considered the primary pollinators of various magnoliid genera and species of *Magnolia* (Baker and Hurd 1968; Delpino 1875; Dieringer and Espinosa 1994; Gibbs et al. 1977; Heiser 1962; Kikuzawa and Mizui 1990; Leppik 1975; Thien 1974). In this study beetles accounted for 10.8% of all insect visits. Beetles consistently carried far less pollen than the bees, and frequently carried pollen of other species (Table 3). The hymenopterans in this study comprised 74.2% of the total insect fauna observed on *Magnolia* flowers. *Apis mellifera* outnumbered other insect visitors and accounted for 70.7% of all insect visits. Honey bees are not indigenous to North America; however, they were attracted to the flowers of *M. grandiflora* and were capable of pollinating the flowers. This suggests that their behavior is similar to the native pollinators. At all three sites, native *Lasioglossum bruneri* were second only to honeybees in relative importance and thus may be a common natural pollinator of *M. grandiflora* (Table 4, 5).

Beetles were floral visitors and carried pollen. They may have transferred pollen by a "mess and soil" pollination syndrome.

Bees, however, were frequent floral visitors and carried large amounts of pollen. Bees were the only pollinators that exhibited behavior in the flowers that was associated with the changes in sex expression, stigmatic receptivity, and changes in pollinator attractants and rewards over the flowering period. The changes in sex expression, stigmatic receptivity, shifts in UV reflectance of floral parts, and pollinator rewards, coupled with the influence these changes had on the behavior of the hymenopteran visitors in the flowers, suggests that despite its size and its presumed archaic flower morphology, *Magnolia* has evolved specialized floral features that effectively influence the foraging behavior of more specialized pollinators (i.e., bees).

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# THE TAXONOMY OF *CAREX* SECTION *SCIRPINAE* (CYPERACEAE)

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ABSTRACT. Section *Scirpinae,* as treated herein, forms a cohesive group of dioecious, unispicate sedges with pubescent perigynia, chromosome numbers of $n = 31$, and similar leaf anatomy, and possesses a high degree of interfertility between subspecies based on hand-pollinations. Taxa in this section are distributed primarily in North America. Taxonomic problems in the group have been related to the lack of a comprehensive monographic treatment, incomplete descriptions, and a lack of an understanding of the patterns of variation in morphological characters across a wide geographic range. Based on evidence from a previous study using morphology, chromosome numbers, leaf anatomy and surface structure, achene and perigynium micromorphology, interbreeding relationships, ecology, and distributions, five taxa are recognized. The section, as treated here, consists of *C. scirpoidea,* with four subspecies (ssp. *scirpoidea,* ssp. *convoluta,* ssp. *pseudoscirpoidea,* and ssp. *stenochlaena*), and *C. curatorum.* Two taxa, *C. gigas* and *C. scabriuscula,* have been excluded.

Key Words: Cyperaceae, *Carex, Carex curatorum, Carex gigas, Carex scabriuscula, Carex* section *Scirpinae, Carex scirpoidea, Carex scirpoidea* ssp. *scirpoidea,* ssp. *convoluta,* ssp. *pseudoscirpoidea,* and ssp. *stenochlaena,* systematics, taxonomy

The taxonomic treatment of *Carex* section *Scirpinae* presented here recognizes *C. scirpoidea* Michx. ssp. *scirpoidea,* ssp. *convoluta* (Kükenthal) Dunlop, ssp. *pseudoscirpoidea* (Rydberg) Dunlop, ssp. *stenochlaena* (Holm) Löve and Löve, and *C. curatorum* Stacey. The subspecies of *C. scirpoidea* are geographically based ecotypes that differ morphologically in only a few characters. Two taxa, *C. gigas* (Holm) Mackenzie and *C. scabriuscula* Mackenzie, previously assigned to the section, have been excluded based on inconsistencies in characters that distinguish the section (Dunlop 1990).

This taxonomic treatment is based on the results of a biosystematic study of the section *Scirpinae* (Dunlop 1990). A detailed analysis of variation in characters focused on morphology, anatomy, achene and perigynium micromorphology, chromosome number, ecology, breeding relationships, and distribution patterns. Specimens were borrowed from 48 herbaria and collected from 30 field sites. At each field site, four to ten plants of each gender were collected and grown in the University of New Hampshire greenhouse for the chromosome analysis, breeding system observations, and crossing experiments. In addition, 17 analyses were conducted on field-site soil samples.

Variation was assessed in a macromorphological study consisting of 139 individuals using 69 qualitative and quantitative characters. A numerical analysis was conducted on a subset of these individuals using Principle Components Analysis.

Achene micromorphology was examined in 62 specimens, resulting in distinctions at the specific level but not the subspecific level (Dunlop 1990). In addition, micromorphological features of 42 perigynia were studied. *Carex scirpoidea* and *C. curatorum* have hirsute to villous perigynia with long hairs distributed over the entire adaxial and abaxial surfaces, or occasionally on the upper one-half to two-thirds surface. This contrasts with *C. gigas* and *C. scabriuscula,* which have sparsely pubescent perigynia with short hairs on the top third of the perigynia.

Internal foliar anatomy and surface features were examined in transverse sections and epidermal peels. The leaves of the subspecies of *Carex scirpoidea* are anatomically indistinguishable except for the very narrow, flanged, V-shaped leaves of ssp. *convoluta.* The presence of hairs on the adaxial leaf surfaces of *C. curatorum* distinguish it from *C. scirpoidea.*

Thirty reliable chromosome counts were made from greenhouse-grown plants; photographic vouchers are presented in Dunlop (1990). The subspecies of *Carex scirpoidea* have counts of $n = 31$, whereas *C. gigas* and *C. scabriuscula* have counts of $n = 29$. Based on the reported aneuploid series in *Carex,* it would not be unexpected to find $n = 29$ as part of a series with $n = 31$. Thus, this lower number alone would not be justification to exclude the two previously mentioned taxa from the group. However, when correlated with morphological, anatomical, and ecological data, chromosome data strengthen the evidence to remove *C. gigas* and *C. scabriuscula* from the section (Dunlop 1990).

Observations on greenhouse-grown plants (Dunlop 1990) show the dioecious breeding system to be stable in *Carex scirpoidea* subspecies and *C. curatorum.* Slight variation occurs whereby one to two staminate flowers may appear among the pistillate flowers on a pistillate spike, or one to three pistillate flowers may occur at the base of a staminate spike or in the axil of the involucral bract. The breeding system of *C. gigas* and *C. scabriuscula* is more variable as plants may often possess small androgynous spikes.

Interbreeding relationships were examined using experimental hand-crosses with greenhouse-grown plants. Subspecies of *Carex scirpoidea,* although rarely sympatric, are highly interfertile in the greenhouse (Dunlop 1990).

## TAXONOMIC HISTORY

Tuckerman (1843) first applied the epithet *Scirpinae* to one of nine groups of sedges of unspecified rank under section *Psyllophorae.* He distinguished the *Scirpinae* as a group of plants that were almost always dioecious with red-brown, pubescent perigynia. His concept of the *Scirpinae* included *C. scirpoidea* (= *C. scirpina* Tuckerman) and *C. drummondiana* Dew. Later, in a treatment of North American carices, Bailey (1887) took a broad view and assigned *C. scirpoidea* to section *Sphaeridiophorae* Drejer, which included subsections *Filifolia* Tuckerman and *Montanae* Fries. In the same year, Pax (1887) placed *C. scirpoidea* in section *Dioicae* Fries in subsection *Scirpoideae.* Kükenthal (1909) adopted Tuckerman's concept of the *Scirpinae* group, excluded *C. drummondiana,* and established section *Scirpinae* in subgenus *Primocarex.* The sectional name is validly published by Kükenthal.

The subgeneric placement of the section *Scirpinae* has varied depending on an author's view of whether the unispicate condition was primitive or derived, or of the evolutionary significance of certain characters (Krechetowich 1935; Kükenthal 1909; Nelmes 1951; Reznicek 1990). Kükenthal (1909) placed the section in subgenus *Primocarex,* as he viewed the unispicate condition as primitive. In a thorough discussion, Reznicek (1990) summarizes the subgeneric history of *Carex* and, as generally agreed, recognizes three subgenera: *Carex, Indocarex,* and *Vignea.* Subgenus *Primocarex* is considered artificial and therefore not recognized due to the heterogeneity of the unispicate *Carex.* Relationships of section *Scirpinae* to other sections remains uncertain.

Since 1803, when Michaux described *Carex scirpoidea,* the taxon on which the section is based, nine additional taxa have been recognized by various authors. Rydberg (1900) recognized *C. pseudoscirpoidea* Rydb. as a distinct species differing from eastern *C. scirpoidea* in being more robust plants with scales shorter than the perigynia. Then, Holm (1904) described two new varieties of *C. scirpoidea*: var. *stenochlaena* Holm and var. *gigas* Holm. Two additional taxa, *C. scabriuscula* Mack. and *C. scirpiformis* Mack., were recognized and described by Mackenzie (1908) in a treatment of *C. scirpoidea* and allies. Kükenthal (1909) recognized two additional varieties of *C. scirpoidea,* var. *convoluta* Kük. and var. *europaea* Kük. Later, Stacey (1937) described *C. curatorum* Stacey, and Hermann (1957) described *C. athabascensis* Hermann.

All but two of the above mentioned taxa (*Carex athabascensis* and *C. scabriuscula*) have been treated by different authors at the specific level or as varieties of *C. scirpoidea.* In his worldwide monograph, Kükenthal (1909) took a narrow view of the section and recognized only one species with five infraspecific taxa (var. *scirpoidea,* var. *europaea,* var. *convoluta,* var. *stenochlaena,* and var. *gigas*). In contrast, in a treatment of North American carices, Mackenzie (1935) recognized six distinct species.

In addition to differing taxonomic viewpoints, various interpretations in terminology, primarily in the use of the words aphyllopodic and phyllopodic, have further complicated our understanding of the systematics of this group. Furthermore, species descriptions have been based primarily on pistillate plants; staminate material often had not been described, nor even observed, for some taxa. Until this study, patterns of variation in morphological characters had not been described across the full geographic range, and information on endemic taxa was sparse.

## TAXONOMIC CRITERIA

This study follows the criteria and definitions of species and infraspecific taxa outlined by Standley (1985) and Crins and Ball (1989) for *Carex.* Species are defined as groups of populations that are distinguished by discontinuities in a suite of morphological and anatomical characters. Additionally, species have a unique geographic distribution or ecology, and are reproductively isolated through either genetic incompatibilities, geographic or ecological isolation, or differences in phenology.

The rank of subspecies has been applied here to the well-defined subunits of the wide-ranging *Carex scirpoidea.* Each subspecies is distinguished by vegetative or reproductive characters, a distinct distribution, and a unique habitat. Four subspecies are recognized, two of which have been designated recently (Dunlop 1997).

## TAXONOMIC TREATMENT

*Carex* L. section *Scirpinae* (Tuckerm.) Kükenthal in Engler, Pflanzenreich 38 (IV:20): 81. 1909. TYPE: *Carex scirpoidea* Michx. *Scirpinae* Tuckerman, Enum. Meth. Caricum Quarunum, 1843. *Scirpoideae* Pax in Engler and Prantl, Nat. Pflanzenfamilien 2(2): 123. 1887, as subsection. *Trysanolepis* V. Krecz. in Komarov, Flora of the USSR 3: 243. 1935.

Cespitose perennials with red-brown, lignescent roots. Rhizomes either short or elongate with internodes 1–2 cm long. Culms arising from current year shoots (lacking the withered persistent leaf bases of the previous year) or from shoots of the previous year, triangular, scabrous on the angles, height exceeding the length of the leaves. Pistillate culms 5–94 cm tall. Staminate culms 3–74 cm tall. Leaves of the rhizome and culm base reduced to sheaths, lacking blades. Leaves of the flowering shoot attenuate, adaxial surface glabrous or pubescent, scabrous with marginal prickles. Vegetative leaves similar to leaves of the flowering shoot; mouth of the leaf sheaths concave, entire to erose; sheath front membranous, scabrous, white to tan; dorsal surfaces coriaceous, glabrous, pale green to red-brown; ligules semicircular to triangular, tan to red-brown, ciliate. Inflorescences unisexual, rarely bisexual, then only with few staminate flowers interspersed in the pistillate spike or 1–2 perigynia in the axils of the involucral bract at the base of a staminate spike. Inflorescences unispicate, very rarely with a small lateral sessile spike of the same sex, erect or on lax culms, linear to clavate, densely flowered to loosely-flowered at the base. Involucral bracts usually present, sometimes single, foliaceous or scale-like, shorter than or equal to the inflorescence, attenuate, inserted below spike. Perigynia ovate to lanceolate, narrower than, equal to or as wide as the subtending scale, tightly or loosely enveloping the achene, pale green, tawny, red-brown to purple-black, hirsute to villose with white-golden brown hairs. Achenes brown, trigonous, 1–2.5 mm long, 0.8–1.5 mm wide, rarely with a short stipe, filling the full length and width of the perigynia or filling only one ⅓ to ½ the length and width. Stigmas 3. Rachilla absent or present. Anthers 1.5–3.5 mm long. Chromosome *n* = 31.

### KEY TO *CAREX* SECTION *SCIRPINAE*

1. Achenes not filling the full length or width of the perigynia, occupying ⅓ the width of the perigynia such that the sides of the perigynia are compressed; adaxial leaf surfaces sparsely pilose with fine white hairs; plants of low elevations in n. Arizona and s. Utah ...... 2. *C. curatorum*

1. Achenes filling the perigynia or at least all but the upper ⅓; adaxial leaf surfaces glabrous; plants widely distributed especially in calcareous soils in arctic and alpine habitats, often on cliffs and ledges ........................ (2)

  2. Culms arising from shoots of the previous year such that withered leaf bases of the previous year persist, sheathing the base of the culm; scale leaves absent at the base of the culm; leaves of the flowering shoot clustered, diverging from one region of the shoot axis ca. 10–20 mm above the rhizome ......................... ............ 1b. *C. scirpoidea* ssp. *pseudoscirpoidea*

  2. Culms arising from shoots of the current year, lacking withered leaf bases from the previous year; scale leaves present, conspicuous at base of the culm, red-brown (anthocyanic); leaves of the flowering shoot diverging from intervals scattered along the shoot axis .... (3)

    3. Perigynia lanceolate to oblanceolate, (2.8) 3–4 (5) mm long, greater than 2.5 times as long as wide; culms usually lax causing the spikes to droop ....... .............. 1d. *C. scirpoidea* ssp. *stenochlaena*

    3. Perigynia ovate to obovate, (1.8) 2–2.5 (3) long, less than 2.5 times as long as wide; culms stiff, spikes erect .................................. (4)

      4. Widest leaves of the flowering culm of pistillate plants more than 1.5 mm wide, leaves flat or widely V-shaped in cross-section .......... ............. 1a. *C. scirpoidea* ssp. *scirpoidea*

4. Widest leaves of the flowering culm of pistillate plants less than 1.5 mm wide, leaves mostly convolute or narrowly V-shaped in cross-section . . ............. 1c. *C. scirpoidea* ssp. *convoluta*

1. **Carex scirpoidea** Michx. Fl. Bor. Am. 2: 271. 1803.

1a. **Carex scirpoidea** Michx. ssp. **scirpoidea**, *C. michauxii* Schwein., Ann. Lyceum Nat. Hist. N.Y. 1: 64. 1824 (based on *C. scirpoidea*). *C. scirpina* Tuckerman, Enum. Meth. Caricum Quarundum 8. 1843 (spelling change, based on *C. scirpoidea*). TYPE: CANADA. Boreal regions, *Michaux s.n.* (HOLOTYPE: P, microfiche P!, photo MT!).

*C. wormskiolidiana* Hornemann, Fl. Dan. 9: 6 pl. 1528. 1816. TYPE: GREENLAND. Mallenefield (Plate 1528).

*C. scirpoidea* forma *basigyna* Lange, Consp. Fl. Groenl. ed. 2:132. 1890. TYPE: not known.

*C. scirpoidea* var. *europaea* Kükenthal, in Engler, Pflanzenreich 38 (IV: 20): 81. 1909. TYPE: NORWAY. Solvagtind, *Kneuker 181* (not seen).

*C. scirpiformis* Mackenzie, Bull. Torrey Bot. Club 35: 270. 1908. *C. scirpoidea* var. *scirpiformis* (Mackenzie) O'Neill & Duman, Rhodora 43: 417. 1941. TYPE: CANADA. Alberta: Banff, damp ground near Middle Spring, 28 Jun 1899, *McCalla 2348* (HOLOTYPE: NY!; ISOTYPE: CU! WTU!).

*C. athabascensis* Hermann, Leafl. W. Bot. 8: 111. 1957. TYPE: CANADA. Alberta: Jasper National Park, on mossy rocky shelf on marl upper shore of Athabaska River above Athabaska Falls, alt. 3800 ft., 20 miles southeast of Jasper, 28 Aug 1956, *Hermann 13498* (HOLOTYPE: US!; ISOTYPES: ALTA!, CAN!, MICH!, NA).

Rhizomes short and creeping. Culms one to several per node, arising from current year shoots (lacking the withered persistent leaf bases of the previous year), scabrous especially at apex. Pistillate culms 0.3–1 mm wide at top, (0.6) 0.8–1.7 mm at base, (5) 10–35 (40) cm tall. Staminate culms 0.5–1 mm wide at the top, 0.8–1.4 mm at base, (3) 9–14 (26) cm tall. Leaf sheaths of the rhizome and the culm bases red-brown to brown-black, glabrous, shiny, coriaceous. Leaves of the flowering shoots 2–5, not clustered along the stem, adaxial surface glabrous, margins scabrous especially towards apex; in pistillate plants (3.5) 11–20 cm long, 1.5–3 (3.4) mm wide; in staminate plants 8–25 cm long, 0.8–2.6 mm wide. Vegetative leaves 5–8 per shoot; in pistillate plants (5) 13–24 (31) cm long, (1.1) 1.5–2.5 (2.7) mm wide; in staminate plants 8–25 cm long, 0.8–2.6 mm wide; ligules semicircular, (0.5) 1–2

(2.3) mm in height, 0.2–0.4 mm wide. Inflorescences unisexual, unispicate, (very rarely with a short sessile lateral spike of the same sex), erect, linear, densely flowered; pistillate spikes (7.5) 10–30 (37) mm long, 3–5 mm wide; staminate spikes 10–25 mm long, 0.5–0.8 mm wide. Involucral bracts usually present, foliaceous or scale-like, shorter than the inflorescence, 3.5–20 cm long, base inserted 2.5–17.5 mm below spike, auriculate. Pistillate scales ovate, (1.5) 1.8–2.5 (2.9) mm long, 1–1.5 mm wide, shorter than, equal to, or longer than the perigynia, apically acute to obtuse, red-brown to brown-black with narrow to broad hyaline margins; central midrib narrow, green-tawny to dark brown, shorter than or extending to apex; margins entire, often ciliate. Staminate scales similar to pistillate, 3.5–4.3 mm long, 1–1.3 mm wide. Perigynia ovate, (1.8) 2–2.5 (3) mm long, (0.9) 1–1.2 (1.5) mm wide, as wide as the subtending scale, abruptly contracted to a beak, generally lacking a short basal stipe, adaxial surface with few obscure short nerves at base, marginal veins not evident, pale green to tawny, becoming red-brown towards apex, hirsute to villose with white hairs; body tightly enveloping the achene; beak 0.1–2 mm long, red-brown and hyaline at tip, straight at maturity, orifice entire and circular. Achenes dark brown, (1) 1.5–1.8 mm long, (0.6) 0.8–1.2 (1.5) mm wide, lacking a stipe, filling the perigynia or at least ¾ the length and width. Rachilla absent. Anthers 1.5–2.5 (3) mm long.

DISTRIBUTION. *Carex scirpoidea* ssp. *scirpoidea* is the most widely ranging taxon in section *Scirpinae* (Figure 1). This subspecies is distributed across northern North America from Greenland, Labrador, and Newfoundland west to the Northwest Territories and Alaska, south to northern New England, northern New York, northern Ontario, northwestern Minnesota, North Dakota, and in the mountains in Colorado, Utah, Nevada, Montana, Idaho, Wyoming, eastern Oregon, and British Columbia. A number of populations occur in Russia on the Kamchatka and Chukotskiy Peninsulas. One disjunct population occurs on Solvagtind Mountain in Norway.

HABITAT. Most often ssp. *scirpoidea* occurs on wet substrates with a high level of calcium (2058 ppm. to 2.52%; Dunlop 1990). In New England, ssp. *scirpoidea* occurs in widely scattered sites where there is some influence from calcareous parent material,

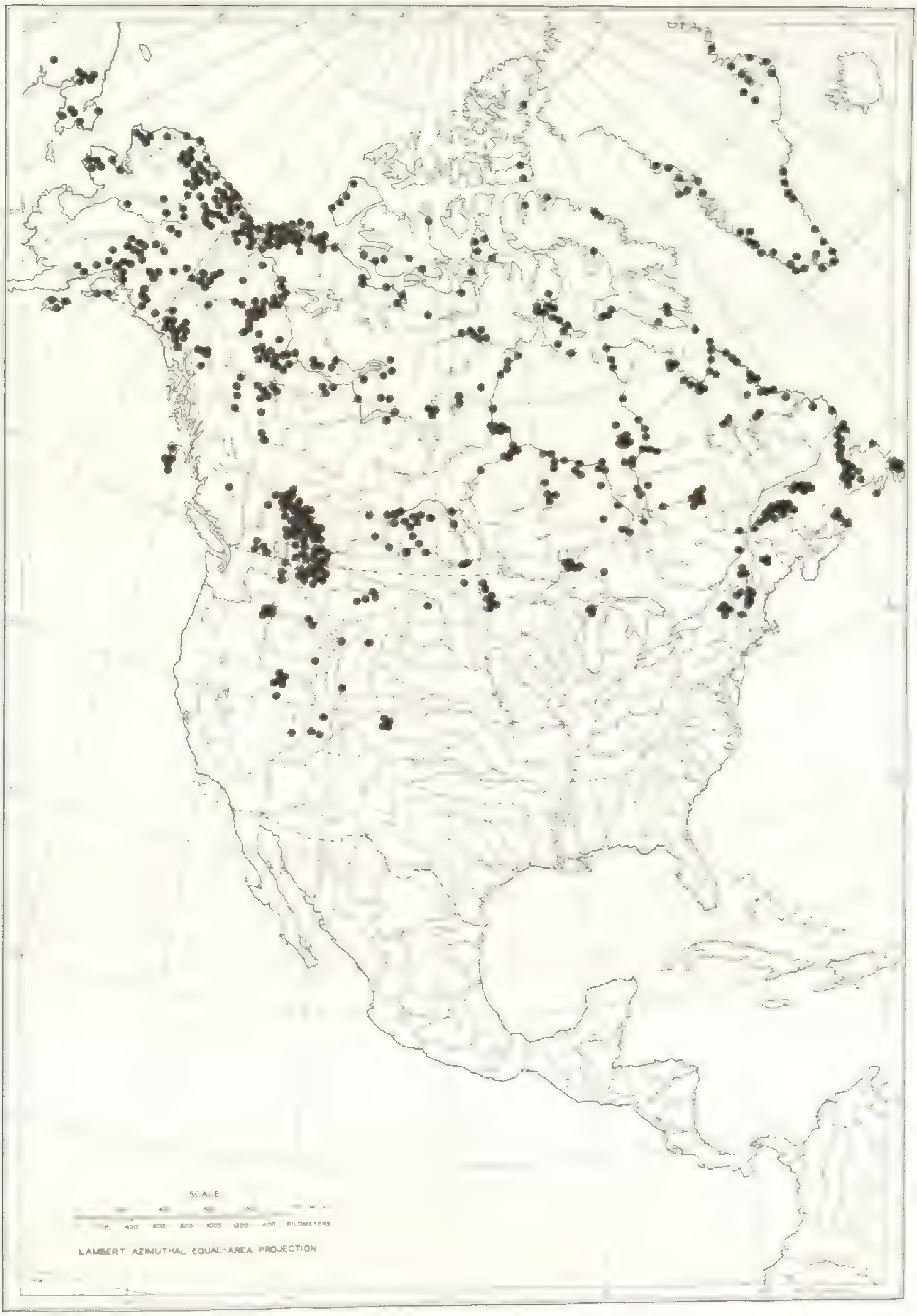
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Figure 1. Distribution of *Carex scirpoidea* ssp. *scirpoidea* in North America and Beringia.

and with associated calcicoles such as *Potentilla fruticosa* L. and *Juniperus horizontalis* Moench. Based on observations in Newfoundland, ssp. *scirpoidea* grows on both calcareous and serpentine substrates.

A specific location is not known for the type, as Michaux (1803) cites the type locality for *Carex scirpoidea* as "ad sinum Hudsonis," and a photo of the type shows a label bearing the locality as "in borealibus Canadae."

*Carex scirpoidea* ssp. *scirpoidea* is the most widespread taxon in this section and includes in synonymy a number of taxa formerly recognized by other caricologists. Kükenthal recognized *C. scirpoidea* var. *europaea* from a single disjunct locality in Norway. Although these plants are short in stature, like typical plants of *C. scirpoidea* ssp. *scirpoidea* from alpine habitats, values for the morphological characters fall within the normal range for ssp. *scirpoidea.* There appears to be no justification for distinct taxonomic recognition for this population.

Another taxon, *Carex scirpiformis,* had been recognized previously by Mackenzie (1908) and treated at the varietal rank by O'Neill and Duman (1941) based on wide, hyaline, pistillate scale margins and light colored pubescence. In addition, Hermann (1957) recognized *C. athabascensis* as a separate species based on the overall robust habit and small, ovoid achenes. These morphological characters of scale margins, pubescence, and size fall into the range of variation for *C. scirpoidea.*

REPRESENTATIVE SPECIMENS: **Canada.** ALBERTA: Brazeau National Forest, Whitehorse Creek, 26–28 Aug 1957, *Porsild 20824* (CAN); Bow River near Pilot Mt., 19 & 26 Jun 1945, *Porsild & Breitung 12304* (CAN); Cline River, on David Thompson Hwy., 27 mi. E of Jasper-Banff Park Boundary, 3 Jul 1968, *Dumais & Anderson 2930* (CAN); Coleman, The Gap, 3 Aug 1957, *Russel 559367* (USAS); Crystal Lake, 31 Jul 1953, *Breitung 17007* (NA); Kananaskis Lakes, along Trans-Canada Highway, upper Marmot Creek Basin, 1 Jul 1963, *Mosquin & Benn 5206* (DAO, SASK); Laggan, 11 Jul 1904, *Macoun 64054* (CAN); Kananaskis Road, 50°13′N, 114°32′W, 30 Aug 1964, *Calder 37292* (DAO); Peyto Lake, 66 mi. N of Banff, 12 Jul 1941, *Weber 2427* (CAN, COLO, GH, WS, UBC); Quartz Ridge, 51°02′42″N, 115°46′10″W, 21 Aug 1972, *Hudson & Scotter 2789* (SASK); Windy Point, 30 mi. W of Nordberg on the David Thompson Hwy., 52°15′N, 116°23′W, 16 Jun 1974, *Dumais 6810* (WAT); North Saskatachewan River, between Mt. Athabaska and Saskatchewan Glacier, near mile 114, 22 Aug 1945, *Porsild & Breitung 14542* (CAN); Sundance pass near Sulfur Mt., 10 Aug 1954, *Ledingham 1954* (USAS); Jasper National Park, Angel Glacier, Mt. Edith Cavell, 4 Aug 1941, *Scamman 2428*

(GH); Jasper National Park, Athabaska River, Athabaska Falls, 20 mi. SE of Jasper, *Hermann 13498* (CAN, MICH); BRITISH COLUMBIA: Alaska Highway, Summit Pass, foot Mt. St. George, mile 392, 10 Aug 1962, *Eastham 118/62* (UBC); Red Mt., W end Quiniscoe Lake, 49°04′N, 120°13′W, 4 Aug 1956, *Calder, Parmelee & Taylor 19782* (DAO, WTU, MIN); 24 mi. E of Golden, Kicking Horse River, 25 May 1938, *McCabe 6297* (CAS, UC); Banff-Windermere Road, near Vermilion Crossing, 11 Jul 1944, *McCalla 8429* (DAO, UBC), *8430* (UBC); Mt. Assiniboine, 32 mi. Banff, Sunburst Lake Camp, 7–17 Aug 1952, *Scamman 6590, 6591* (CAN); Muncho Lake, 2 Jun 1944, *Porsild 9023* (CAN); Mount Robson Prov. Park, Mt. Ann Alice, above Berg Lake, 53°10′N, 119°11′W, 19 Aug 1956, *Jenkins 7235* (DAO); Queen Charlotte Island, Canoe Pass, 26 Jul 1910, *Spreadborough 83090* (CAN); Spinel Lake, 57°50′N, 126°23′W, 4 Aug 1977, *Gillett & Boudreau 17735* (CAN); Wicked River, 56°3′N, 123°40′W, 16 Jul 1932, *Raup & Abbe 3863* (CAN, F, GH, MIN, MT, NY, US); Windermere, slopes Paradise Mine, 31 Jul 1953, *Calder & Savile 11273* (DAO); Yedhe Creek, near 58°33′N, 125°23′W, 10 Jul 1971, *Annas s.n.* (DAO); Yoho National Park, Emerald Lake, 4 Jun 1947, *McCall 9591* (ALTA, UBC); LABRADOR: Anchorstok Bay, 1934, *Potter & Brierly s.n.* (US); Battle Harbour, Rawson-MacMillan Expedition, 1927, *Sewall 195* (GH, F); Cape Mugford, 57°55′N, 61°55′W, 11 Aug 1939, *Dutilly, O'Neill & Duman s.n.* (DAO); Fraser Canyon, Lake Tasisuak, 100 km from Nain, 10 Aug 1973, *Shepard & Matthews 82* (CAN); Gerin Mt., 55°04′N, 67°14′W, 21 Jul 1955, *Viereck 666* (CAN); Hamilton Inlet, Rodney Mundy Island, Indian Head, 54°27′N, 57°12′W, 8 Jul 1931, *Abbe & Hogg 132* (CAN, GH); Hebron, 58°15′N, 62°40′W, 17 Jul, 1939, *Oldenburg 38a* (MIN); Hopedale, 55°27′N, 60°12′W, 25 Jul 1928, *Bishop 147* (CAN, GH); Knob Lake, Schefferville area, 54°45′N, 66°40′W, 23 Jun 1963, *Hustich & Kalio 213* (CAN); Marble Lake, 54°25′N, 66°26′W, 12 Jul 1967, *Mäkinen 67-503* (CAN); Nain, 12 Jul 1937, *Potter 7421* (WIS), 16 Aug 1937, *7425* (WIS); Torngate Region, Kangalaksiorvik, 59°25′N, 63°40′W, 6 Aug 1931, *Abbe 135* (CAN); Rowsell Harbor, 58°58′N, 63°15′W, 20 Jul 1931, *Abbe & Odell 133* (GH); Windy Tickle, 18 Aug 1937, *Walker 1126* (PH); MANITOBA: Brandon, 15 Jul 1951, *Stevenson 366* (DAO); Cowan, 30 mi. E of Swan Lake, 12 Jul 1950, *Scoggan & Baldwin 7966* (CAN); Hudson Bay, 13 Jun 1950, *Brown 631* (NHA); Fort Churchill, 4 Aug 1948, *Gillett 2392* (MAINE); Gillam, 21 Aug 1950, *Schofield 1523* (CAS, DAO, NY, WS); Ilford, 56°20′N, 95°60′W, Jul 1976, *Sims 1108* (CAN); Lake Winnipegosis, between Cedar Lake and Lake Winnipegosis, 17 Aug 1948, *Scoggan 4651* (CAN); Landing Lake, 23 Jul 1951, *Irvine 761* (DAO); Moosehorn, 110 mi. W of Winnipeg, 9 Jul 1951, *Scoggan 9299* (CAN); Nelson River, Gillam Island, about 15 mi. above Port Nelson, 30 Jul 1949, *Scoggan 6267* (ALTA, CAN, GH, MIN, MT), 4–12 Sep 1946, *Tryon & Dahl 129* (MIN); NEW BRUNSWICK: Aroostook River Basins, Aroostook Falls, ledges, (both sides of river according to label), 15 Jun 1940, *Chamberlain 1579* (MAINE, UC); NEWFOUNDLAND: Avalon Pen., Conception Bay, Topsail, 12–19 Aug 1901, *Howe & Lang 1207* (GH, NY); Bear Head, 26 Jul 1951, *Rouleau 2072, 2074* (DAO, MT); Bellburn's limestone barrens on W Rt. 430, 19 Aug 1986, *Dunlop & Orlando 2505* (NHA); Blowmidon Mts., roadside, 1.8 mi. W of Rattling Brook on Rt. 460, 19 Aug 1986, *Dunlop & Orlando 2473* (NHA); Bonne Bay, Shag Cliff, 9 Aug 1929, *Fernald, Long & Fogg 1404* (GH, MT, NY); Eagle's Nest

Brook, Mine Brook, York Harbor Mine, 12 Jul 1952, *Rouleau 3064* (MT); Eddie's Cove, 28.4 mi. W of junct. Rt. 345 and new Rt. 430, 23 Aug 1986, *Dunlop & Orlando 2524* (NHA); Frenchman's Cove, 19 Aug 1965, *Rouleau 9946* (MT); 1 mi. W of Steady Brook, 19 Jul 1979, *Hellquist & Crow 13555* (BOSC); Marble Mt., S side facing Humber River on Rt. 1, 19 Aug 1986, *Dunlop & Orlando 2480* (NHA); Point Ritchie, Porte aux Choix, Aug 1986, *Dunlop & Orlando 2510* (NHA); Green Island Cove, 23 Aug 1986, *Dunlop & Orlando 2522* (NHA); Table Mountain radar site, 4 km W, 18 Aug 1986, *Dunlop & Orlando 2440* (NHA); Winterhouse Brook, *Dunlop & Orlando 2481* (NHA); NORTHWEST TERRITORY: Adelaide Peninsula, near E side Sherman Basin, 12 Jul 1957, *MacPherson 66* (CAN); Alexander Falls, Andersen River, reindeer grazing preserve, 69°40′N, 128°57′W, 23 Jul 1965, *Scotter 7070, 7089* (DAO); Burnside Harbour, 12 Aug 1944, *Oldenburg 44-729* (MIN); Baffin Island, Apex Hill, 63°45′N, 67°15′W, 7 Aug 1964, *Swales s.n.* (RM); Arctic Bay, Admiralty Inlet, 12 Aug 1927, *Malte 118543* (CAN); Acadia Cove, Resolution Island, 27 Jul 1937, *Potter s.n.* (WIS); Clyde Inlet, 3 Jul 1950, *Wynne-Edwards 8904* (CAN); Baffin Island, Frobisher Bay, Point Brewster, 3 Aug 1937, *Potter 8294* (CAS); Bathurst Inlet Region, 66°52′N, 108°18′W, 2 Aug 1979, *Scotter & Zoltai 32026* (DAO); Baker Lake, 20 Jul 1963, *Choque s.n.* (MT), 10 Aug 1947, *Freeman s.n.* (DAO); Belcher Island, SW shore Kasegelik Lake, 12 Aug 1959, *Freeman 5062* (TRTE); Point Separation, 68°20′N, 133°30′W, 15 Jun 1927, *Porsild & Porsild 1888* (CAN); Canol Road, mile 111, Bolstead Creek, 25 Jul 1944, *Wynne-Edwards 8252* (CAN); Cape Dalhousie, 70°13′N, 129°40′W, 31 Jul 1963, *Cody 13137* (DAO); Cache Creek, 68°16′N, 136°22′W, 20 Jun 1973, *Welsh & Rigby 12042* (CAN); Cli Lake, 10 Aug 1961, *Cody & Spicer 12204* (DAO, US); Chick Lake, 65°53′N, 128°07′W, 15 Aug 1973, *Gubbe 310(100), 315(99)* (ALTA, SASK); Devon Island, Truelove Inlet, 75°41′N, 84°40′W, 16 Jul 1974, *Mackenzie 18* (CAN); Eskimo Lake, 68°57′N, 132°43′W, 6 Aug 1957, *Cody & Ferguson 10489* (DAO); Ellesmere Island, 78°53′N, 75°50′W, 14 Jul 1979, *Gillett & Schepanek 18105* (COLO); Great Bear Lake, Sawmill Bay, Leith Peninsula, 15–16 Jul 1948, *Shacklette 3032* (MICH, MT, US); Hudson Bay, Kugong Island, 56°11′N, 80°05′W, 29 Jun 1971, *Manning s.n.* (DAO), 5 Jul 1971, *Manning s.n.* (DAO), 7 Sep 1971 (DAO); James Bay, Solomons, Temple Island, 14 Jul 1949, *Baldwin 1657a* (MAINE), *1691* (MAINE, MICH); Jean-Marie River on Mackenzie Highway, 15 Jun 1973, *Skogland 793* (SASK); Coral Harbour, Munn Bay, 9 Aug 1948, *Cody 1959* (MT); Munn Bay, 9 Aug 1948, *Cody 1950* (NA); Murchison River, 67°46′N, 93°52′W, 20 Aug 1975, *Gubbe, Maddison & Burr 862* (SASK); Tehek Lake, 2 Aug 1952, *Oldenburg 52-80* (MIN); Thelon River, 64°45′N, 96°25′W, 27 Aug 1975, *Gubbe, Maddison & Burr 1042* (SASK); Mackenzie River, N peak of Nahanni Mt., 9 Jul 1944, *Wynne-Edwards 8431* (CAN); Lone Mt., 7 Jul 1944, *Wynne-Edwards 8432* (CAN); Carcajou Lake, 64°42′N, 127°55′W, 16 Jul 1965, *Youngman & Tessier 717* (CAN); Coral Peaks, 65°05′W, 129°11′W, 10 Jul 1972, *Cody & Brigham 20715* (DAO); O'Grady Lake, 63°05′N, 128°50′W, 29 Jul 1967, *Cody 16928* (DAO); Redstone River Region, 62°55′N, 126°38′W, 21 Jun 1963, *Kvale & Haggard 43* (DAO); Sekwi Mt., 63°30′N, 128°40′W, 3 Aug 1967, *Cody 17363* (DAO); South Nahanni River, 61°20′N, 124°28′W, 2 Jul 1970, *Scotter 12577* (DAO); Mount Flett, 32 mi. N of Fort Liard, 62°42′N, 123°37′W, 1 Aug 1961, *Cody & Spicer 11884* (DAO); Nahanni

National Park, 61°29′N, 109°28′W, 24 Jul 1976, *Talbot 6110* (CAN); Mistake Bay, 62°05′N, 93°06′W, 20–29 Jul 1930, *Porsild 5638* (CAN); Mt. Sidney, Dobson, 26 Aug 1975, *Scotter & Marsh 5665* (SASK); North Sleeper Island, 59°17′N, 80°40′W, 2 Sep 1939, *Dutilly, O'Neill & Duman 87568* (MO); Norman Wells, Bosworth Creek, 29 Jul 1953, *Cody & Gutteridge 7660* (DAO, F, GH); Rankin Inlet, 62°49′N, 92°05′W, 17 Jul 1973, *Gillett 16067* (CAN); Victoria Island, Cambridge Bay, 12 Aug 1959, *Calder, Savile & Kukkonen 24152* (DAO); NOVA SCOTIA: Inverness Co., Corney Brook, 29 Aug 1956, *Webster 633* (CAN, DAO, MT); LeBlanc Brook, Cheticamp River, 6 Jul 1953, *Smith et al. 7754* (MT), 28 Aug 1956, *Webster 630* (CAN, DAO, MAINE); Victoria Co., Salmon River, Lockhart Brook, 8 Jul 1952, *Smith et al. 6385* (DAO); Cape Breton Co., North Sydney, Cape Breton, 13 Jul 1883, *Macoun 31-835* (CAN); ONTARIO: Cochrane District, Albany River, 51°13′N, 84°22′W, 7 Aug 1960, *Dutilly & Lepage 38558* (DAO); Mammammatawa, 50°16′N, 84°47′W, 2 Aug 1960, *Lepage 38340* (DAO); North French River, 50°26′30″N, 81°03′W, 20 Jul 1979, *Riley 11026* (CAN); Kenora District, Aquatuk Lake, Patricia Portion, 54°21′30″N, 84°36′W, 11 Aug 1980, *Riley 11763* (MICH); Black Duck River, 19 Jul 1953, *Moir 1939* (CAN, MIN); Brant River, 22 May 1973, *Maycock 19226* (TRTE); Goose Creek, Hudson Bay, 18–20 Aug 1952, *Moir 1556* (MIN); James Bay, River Opinaga, 54°12′N, 26 Aug 1953, *Lepage 31622* (DAO); Jigsaw Islands, 13 Jul 1958, *Baldwin 7631* (CAN); Henrietta-Maria, Hudson Bay, 54°48′N, 82°20′W, Jul 1979, *Sims 2649b* (MICH); James Bay, Winisk River, 55°05′N, 85°20′W, 10 Aug 1962, *Dutilly & Fernette 40003* (MT); James Bay, Albany River, 7 Aug 1960, *Duman 38578* (MY); Thunder Bay District, Lake Nipigon, Flat Rock Portage, E side of South Bay, 26 Jul 1960, *Garton 7797* (MSC, MT, NHA); Thunder Cape, 48°20′N, 88°50′W, 31 Jul 1936, *Taylor, Losee & Bannan 1473* (CAN, GH); Terrace Bay, 48°46′N, 87°07′W, 13 Jul 1966, *Parmellee & Savile 3646* (DAO); Mortimer Island, Bernard Point, 48°40′N, 87°04′W, 30 Jun 1973, *Given & Soper 73166* (MICH); QUEBEC: Black Lake, Caribou Hill, 16 Jul 1951, *Raymond et al. 1457, 1626* (DAO, MT); Caribou Lake, 20 May 1965, *Blais et al. s.n.* (CAN, SASK); Coleraine, 3 Aug 1977, *Beach 43* (TRTE); Diana Bay, 10 Aug 1936, *Ney & Courtright 2404* (CAN); Fort Chimo, 22 Jul 1963, *Legault 6770* (DAO, MT, SASK); Great Whale River, 2 mi. N of Hudson Bay Post, 55°17′N, 77°47′W, 1 Aug 1949, *Savile 562* (MT, NA); Marble Mountain, North Canton, 19 May 1970, *Hamel, Forest & Brisson 70048* (DAO); Mont Caribou, 7 Jun 1981, *Blondeau s.n.* (CAN); Mont Logan, 20 Jun 1948, *Levesque 48400* (DAO); Shickshock Mts., 27 Aug 1882, *Macoun 31-836* (CAN); Mistassini Territory, Lake Albanel, Presqu'île Sylvie, 51°5′44″N, 73°43′W, 1–7 Aug 1944, *Rousseau & Rouleau 1227* (MT); Gaspé, Bonaventure Co., Bonaventure River, 2–9 Aug 1904, *Collins, Fernald & Pease 5795, 5934, 5935* (GH); Gaspé-Est Co., Ile Bonaventure, 28 Jul 1950, *Fabius & Allyne 3029* (DAO); 3 mi. W of Cap-des-Rosiers-Est, 18 Aug 1971, *Morisset 71-581* (CAN); Grand River, 21 Jul 1975, *Churchill 722104* (MSC); Mt. Percé, 25 Jul 1905, *Williams, Collins & Fernald* (GH, MIN); Petit Pabos River, 2 Jul 1941, *Scoggan 1802* (CAN); Gaspé-Ouest Co., Mont Albert, 21 Jul 1906, *Fernald & Collins s.n.* (CAN, GH, MSC, MT, VT, US); Saint Ann River, Parc de la Gaspésie, 31 Jul 1956, *Raymond 68192* (MT); L'Ile d'Anticosti, Cirque à la Chaloupe, 7 mi. from ocean, 14 Jul 1942, *Rousseau 52282, 52283* (MT); Rivière du Brick, 23 Jul 1927, *Marie-Victorin & Rolland-Germain 27-*

*510, 511* (CAN, CAS, F, MO, MT, NY, PH, WS); Rivière Chicotte, 24 Jul 1927, *Marie-Victorin & Rolland-Germain 27-512* (CAS, MT, MO, NY, UC, WIS); Rivière à la Patate, 25 Jul 1925, *Marie-Victorin et al. 20100* (MT, NY, WIS, US); Rivière au Saumon, 11 Aug 1927, *Marie-Victorin & Rolland-Germain 27-509* (MO, MT, US); Rivière Pavillon, 17 Jul 1942, *Rousseau 52313* (MT); Rivière Vaureal, 27 Jul 1925, *Marie-Victorin & Rolland-Germain 20495, 20496, 20497* (MT, US, NY); Matane Co., Mt. Collins, Nettle Gully, 9 Jul 1923, *Fernald et al. 25509* (CAN, CAS, F, GH, MO, MT, NY, UC, US); Mt. Pembroke, *Kowal 78* (WIS); Cape Jones, N of portage, 24–25 Jun 1947, *Baldwin, Hustich, Kucyniak & Tuomikosky 333* (CAN, WS); James Bay, Opinaca River, 54°12′N, 26 Aug 1953, *Dutilly 31622* (MT); South Twin Island, 53°8′N, 80°00′W, 15 Jul 1929, *Porsild 4213* (CAN); Solomons Temple Island, 14–17 Jul 1949, *Baldwin 1657, 1693* (CAN); Bear Island, 17 Aug 1947, *Coates s.n.* (CAN); Pte. au Huard, Pint Hills, 11 Jul 1947, *Baldwin et al. 334* (CAN); Port Harrison, 58°17′N, 78°10′W, 18–20 Aug 1928, *Malte 120819* (CAN); Richmond Gulf, 14 Aug 1944, *Lepage & Dutilly 13103* (GH); Smith Island, east coast of Hudson Bay, 60°47′N, 78°36′W, 24 Aug 1928, *Malte 120899* (CAN, GH, MT); Ungava District, Knob Lake near Lake Gillard, 16 Aug 1948, *Hustich 540* (GH, MT); Payne River, near 60°N, 71°25′W, 11 Aug 1948, *Rousseau 1121, 1143* (MT); Portland Island, 55°20′N, 78°50′W, 13 Sep 1939, *Dutilly, O'Neill & Duman 87948* (BH, DAO, GH, MIN, MT, PAC); Porpoise Cove, Hopewell Sound, 10 Sep 1939, *Dutilly, O'Neill & Duman 87799* (USAS, US); Port Manvers, 56°58′N, 61°23′W, 9 Aug 1939, *Dutilly, O'Neill & Duman 7726* (DAO); Mont Reed, 52°1′N, 68°05′W, 20 Jul 1961, *Landry 762* (MT); Ungava Bay, near Korok Bay, 21 Jul 1951, *Rousseau 416* (MT); Windy Tickle, 55°46′N, 60°20′W, *Dutilly, O'Neill & Duman 7459* (US); Walrus Point, 13 Jul 1947, *Baldwin et al. 336* (CAN); Wakeham Bay, 61°40′N, 72°5′W, 30 Jul 1928, *Malte 120262* (CAN); SASKATCHEWAN: Churchbridge, E of Yorktown, Grand Trunk Pacific Railway, 4 Jul 1908, *Macoun & Herriot 72763* (GH, US); Dry Lake, 12 mi. S of Indian Lake, 16 Jun 1964, *Ledingham et al. 3736* (DAO); Hasbala Lake, 59°55′N, 102°05′W, 13 Jul 1963, *Argus 173-63* (CAN, DAO, GH, SASK); Insinger, 5 mi. N, 15 Jun 1952, *Boivin & Alex 9313* (DAO, SASK); Kisbey, 13 Jul 1951, *Boivin & Dore 7821* (DAO); Lipton, *Clokey 294* (UC, US); McIntyre Creek, 1 mi. E of Quantock, 7 Aug 1980, *Ledingham 6840* (USAS); Muenster, 11 Jul 1928, *Ledingham s.n.* (SASK); Mortlach, 12 Jun 1950, *Ledingham 791* (USAS); Paterson Lake, 59°55′N, 102°20′W, 27 Jul 1963, *Argus 443-63* (SASK); Patience Lake, 3 Jun 1940, *Ledingham s.n.* (SASK); Prince Albert, 19 Jun 1949, *Ledingham 49-251* (MT, SASK, USAS); Quillwort Lake, S of Hasbala Lake, 59°54′N, 102°05′W, 28 Jul 1962, *Argus 843-62* (SASK); Raymore, 12 mi. N of Tower, 4 Jul 1976, *Hudson 3166* (DAO, SASK, USAS); Watson, 19 Jul 1952, *Russell 521-87* (DAO); Wiseton, 27 May 1978, *Hudson 3513* (DAO, SASK, USAS); E of Yorkton on Grand Trunk Pacific Railway, 4 Jul 1906, *Macoun & Herriot 72763, 72764* (F); YUKON TERRITORY: Atlin Lake, 60°22′N, 133°51′W, 19 Aug 1943, *Raup & Correll 11438* (MICH); Blackstone Valley, along Dempster Hwy. mile 83, 4 Jul 1968, *Porsild 1513* (CAN); Boulder Creek, 68°27′N, 138°13′W, 22 Jun 1974, *Nagy & Goski 74-159* (DAO); Bridge Creek, 61°35′N, 138°50′W, 6 Jul 1948, *Raup, Drury & Raup 13345* (AA, CAN, GH); British Mountains, 69°13N′, 139°37′W, 21 Jul 1972, *Wein et al. 264* (DAO); 90 mi. NW of Dawson City, SE of Mt. Klotz, 62°21′N, 140°06′W, 6 Jul 1973, *Greene 386, 389* (ALTA, DAO); Donjek River, 11 Aug 1927, *Müller s.n.* (NY); Firth River, 69°22′N, 139°25′W, 18 Jul 1972, *Wein et al. 269c* (DAO); Kaskawulsh Nunatak, jct. of N and central arms Kaskawulsh Glacier, W of Kluane Lake, Jul–Aug 1965, *Murray & Murray s.n.* (DAO); Kluane National Park, Bullion Creek-Sheep Creek Plateau, ca. 7 km NW of Slims River, 3 Jul 1975, *Douglas 8471* (DAO); Lapie Lake, near mile 105, Rose-Lapie R. Pass, 10 Jun 1944, *Porsild & Breitung 9290* (GH); McQuesten area, 63–64°N and 136–138°W, 12 Aug 1948, *Campbell 809* (CAN); mile 123 Haines Highway, (ca. 6.5 km W), 11 Jul 1975, *Weaver 137, 138* (DAO); 24-mile Cabin on 60-mile Road from West Dawson to Alaskan border, 64°13′N, 140°06′W, 15 Aug 1949, *Calder 4517* (CAS, RM, MT, NA, WS); 60-mile Road, 57 mi. from Dawson to Alaskan border, 64°05′N, 140°53′W, 9–10 Jul 1949, *Calder & Billard 3590* (DAO); mile 85 Haines Road, 17 Jul 1944, *Clarke 554* (CAN); Mt. Caribou, N of Carcross, 60°14′N, 134°42′W, *Calder 4528* (MT); Mt. Sedgwick, British Mts. 68°53′N, 139°06′W, 19 Jul 1962, *Calder 34460* (DAO); Mt. Schaeffer, 67°43′N, 139°48′W, 10 Aug 1971, *Wein et al. 142d* (DAO); Mt. White 7 mi. E of Little Atlin Lake, 19 Aug 1943, *Raup & Soper 11438* (SASK); Old Crow Flats, 68°15′N, 138°50′W, 11 Jul 1970, *Welsh & Rigby* (NY); Ogilvie Mts. 65°37′N, 138°56′W, 26 Jul 1960, *Calder & Gillett 26004* (DAO); 52 mi. NE of Dawson, 15 Jul 1963, *Youngman & Tessier 342, 343* (CAN); Ptarmigan Heart, 61°49′N, 138°35′W, 16 Jul 1948, *Raup, Drury & Raup 13701* (AA, CAN, MICH); Red Tail Lake, 61°50′N, 138°52′W, 9 Jul 1948, *Raup, Drury & Raup 13469* (AA, CAN); Ruby Range, Gladstone Creek, 61°17′N, 138°36′30″W, 12 Jul 1966, *Neilson 816* (CAN); St. Elias Mts., Dezadeash River Valley, 3 Jun 1967, *Pearson 67-22* (CAN); Sam Lake, 13 Jul 1974, *Nagy & Pearson 74-304* (DAO); Spruce Creek, 19 Jul 1974, *Nagy & Pearson 74-477* (DAO); Yeiken River, Rink Rapids, 9 Jul 1902, *Macoun 53898* (CAN, NY); White River on Alaska Hwy., 21 Jul 1944, *Anderson 9308* (CAN, GH).

**Miquelon.** (French) Cape Miquelon, 27 Jul 1937, *Hors 50* (MT), 22 Jul 1942, *Le Gallo 187* (MT); Voiles Blanches, 17 Aug 1939, *Hors 50-a* (MT).

**Greenland.** Arfersiorfih Fjord, 19 Jul 1924, *Porsild s.n.* (CAN, GH, MO, NY, US); Amitsuarssuk, 60°08′N, 44°45′W, 7 Aug 1967, *Hansen, Kliim-Nielsen & Øllgaard 67-1920* (DAO); Angmagssalik Dist., Gingertivag, 14 Jul 1969, *Hamann & Kliim-Nielsen 69-1368* (NY); Battle Harbour, 29 Jun 1883, *Waghorne s.n.* (MO); Cape York, 23 Jul 1894, Peary Auxilliary Expedition, *Wetherill 51* (GH); Disko, Arktiske Station, ca. Neria, 61°33′N, 4 Aug 1931, *Eugenius s.n.* (MT); Disko Island, Mudderbugtsdalen, 69°40′N, 4–5 Aug 1937, *Porsild 377* (CAN); Egalugialik, Itivdleg, 64°21′N, 50°27′W, 5 Aug 1973, *Feilberg s.n.* (NY); Ella Island, Cape Oswald, Ulvedalen, 72°52′N, 25°10′W, 24 Jul 1932, *Sørensen 3120* (CAN); Fiskenaesset, 63°13′N, 50°14′W, 16 Jul 1972, *Andersen & Feilberg 4301* (MO); Gäoseland, Faxe Sø, 70°15′N, 29°W, 21 Jul 1958, *Holmen & Laegaard s.n.* (DAO); Godhaab Gulf, Jordan Hill, 74°07′N, 27 Jul 1930, *Seidenfaden 825* (NY); Hurry Fjord, 70°52′N, 22°30′W, Liverpool Land, 14 Jul 1963, *Taggart s.n.* (CAN); Igdlorssuit, 17 Jul 1966, *Gravesen & Hansen 66-1848* (MO); Ikâsaulaq, 65°59′N, 37°26′W, *Astrup & Kliim-Nielsen 25* (MO); Ikertog, 66°56′N, 52°20′W, 31 Jul 1978, *Moller s.n.* (COLO); Ikerasak Umanaq Distrikt, 70°29′N, 9 Jul 1929, *Porsild s.n.* (CAN, MT); Itivdlerssuaq, 60°10′N, 44°29′W, 28 Jul 1967, *Hansen, Kliim-Nielsen & Øllgaard 67-535* (CAN); Julianehaab, near Søen, 30 Aug 1937, *Grøntved 2114* (DAO); Kangerdlugsuak, Knud Rasmussen Land, Skaergaerd Peninsula, 17 Aug 1936, *Wager & Wager s.n.* (DAO); Kangerssuneq Quigordleq, Anivia, 60°19′N, 44°07′W, 4 Jul 1966, *Hansen 66-1047* (MO); Kjerulf Fjord, 8 Aug 1937, *Oosting 1014* (CAS); Kong Oscars Fjord, 72°14′N, 23°55′W, 1 Jul 1956, *Raup, Raup & Washborn 25* (CAN); Kûngmiut, 60°00′N, 44°28′W, 2 Jul 1967, *Hansen, Kliim-Nielsen & Øllgarrd 67-924, 969* (NY); Praestefjeld, 66°55′N, 53°35′W, 5 Jul 1949, *Gelting s.n.* (COLO); Quinqua, 60°21′N, 23 Jul 1925, *Porsild & Porsild s.n.* (US); Scoresbysund, 71°20′N, 24°40′W, 13 Aug 1937, *Sørensen 259* (MT); Skeldal, 72°15′N, 24°W, 16 Jul 1963, *Spearing et al. 171* (MICH); Söudre Strömfjord, 7 Aug 1927, *Erlanson 2584* (MICH, NY); Tasîssârssik Fjord, 66°05′N, 37°00′W, 14 Jul 1963, *Gribbon 28* (CAN); Tasiusak, 61°45′N, 25 Jul 1889, *Hartz s.n.* (MO); Tasersiaq, Cache Point, 14 Aug 1962, *McCormick 201* (PH); Thafjorden, 11 Aug 1935, *Lagerkranz s.n.* (UC); Tornarssuk, Nûa, 59°54′N, 44°21′W, 1 Aug 1967, *Hansen et al. 67-1794* (PH); Trail Island, Holm's Bay, 11 Aug 1929, *Vaage s.n.* (DAO); Tunugdlairfick, Mâjût, 61°04′N, 45°35′W, 31 Aug 1962, *Hansen, Hansen & Petersen 2235* (DAO); Ymer Island, Botanikerbugten, 73°08′N, 25°10′W, 18 Aug 1932, *Sørensen 3116* (CAN).

**Norway.** Norland Province, Junkerdalen, Salten, Mt. Solvagtind, 66°48′N, 15°35′E, 9 Aug 1859, *Behm s.n.* (UC), 8 Aug 1859, *Schlyter & Behm s.n.* (F, NY) 18 Aug 1883, *Nessen 805* (F), 9 Jul 1948, *Jordal 1202* (F, MICH).

**Russia.** Kamchatka Oblast, Koryaksky National District, Olyutorsky region, Verkhoturova Island, 26 Jul 1975, *Kharkevich & Kozhevnikov s.n.* (ALA, DAO, UBC); Madadam Oblast, Chukotskiy Peninsula, (NE coast) near mouth of Chegitum River, 12 Aug 1971, *Sekretareka, Sitin & Yurtsev* (ALA); middle branch of Erguveem River (left bank) near mouth of Vatamkaivan River, Pepenveem River, 1 Aug 1970, *Nechaeva* (ALA); middle branch of Utaveem River, 25 Aug 1970, *Kozhevnikov, Nechaev & Yurtsev* (ALA); Coast of Bering Strait, Puoten Bay, 21 Aug 1972, *Gorbukova, Makarova & Plieva* (ALA); Amguenii River Valley, middle branch, 87 km Evgekinot-Iul'tin Road, 5 Aug 1970, *Kozlova* (ALA); North part of Gulf of Laurentiya, 13 Aug 1969, *Afonina & Korobsov* (ALA); Iul'tinsk Region, near Egvekinot-Iul'tin Road, 16 Jul 1978, *Razhivin* (ALA); Anadirskii Region, southern extremity of Pekul'nay Mountains, middle branch of southern Pekul'nayevem River, 8 Aug 1979, *Korobkov & Sekretareva* (NY); Anyuiskoye Upland, 15 Aug 1973, *Petrovsky* (ALA); southern spur of Teniah Mts., at source of the Loran River, 14 Aug 1972, *Gorbukova, Makarova & Plieva* (ALA); SW coast of Chukotskiy Peninsula, near Nunligran settlement, 28 Aug 1970, *Afonina, Korobkov, Plieva & Khrenov* (ALA); Anyuiskoye Upland, Pogingen River, 8 Aug 1976, *Petrovsky & Korobkov* (ALA).

**United States.** ALASKA: Alaktak, Half Moon, 70°45′N, 155°00′W, 1 Aug 1949, *Spetzman 2439* (CAN, US); Anaktuvuk Pass, 12–15 Aug 1960, *Hultén s.n.* (GH); Alaska Yukon Boundary, 10 Aug 1961, *Hultén* (NY); Alaktak, 155°N, 70°45′W, *Scholander s.n.* (DAO); Atkasuk, Meade River, ca. 100 km SSW of Barrow, 70°28′N, 157°25′W, 7 Aug 1966, *DeBenedictis 534* (CAN, DAO); Bonanza Creek, Eagle Summit, 16 Jul 1949, *Scamman 5270* (GH); Brooks Range, airstrip at 'Nolan', 19 Jun 1949, *Jordal 1839* (BH, MICH); 46 mi. NNW of Arctic Village, 68°40′N, 146°30′W, 18 Aug 1973, *Hettinger 814* (CAN); Cane Creek, 68°35′N, 144°50′W, 8 Aug 1972, *Hettinger 159*

(ALTA); Cape Beaufort, 3–7 Aug 1961, *Hultén s.n.* (DAO, GH); Chip River, 70°26′N, 154°50′W, 17 Jul 1956, *Wiggins 13674* (DS, US); Chitina River head, 16 Jun 1925, *Laing 20* (CAN); Chugach Mts., Anchorage, 29 Jun 1948, *LePage 23355* (US); Circle Hot Springs, 138 mi. N of Fairbanks, 17–22 Jul 1936, *Scamman 69* (GH); Colville River, 150°45′W, 69°45′N, 10 Aug 1953, *Cantlon et al. 649* (MSC); Delta River, S of Donnely Inn, 10 Aug 1966, *Foote 8075* (RM); Daipaious Creek, 21 Jul 1958, *Packer s.n.* (ALTA); Donnely Dome, mile 250 Richardson Hwy., 63°47′N, 145°45′W, 2 Aug 1951, *Cody 6284, 6286* (DAO); Farwell Lake, 62°33′N, 153°36′W, 3–4 Aug 1949, *Drury 2463* (GH); Fairbanks, Miller House on Steese Hwy., 12–28 Jul 1940, *Scamman 2009* (GH); Firth River, 2 mi. S of junction Firth & Mancha Creek, 11 Aug 1961, *Stone* (RM); Fish Creek, 70°19′N, 151°58′W, 26 Jul 1977, *Murray & Johnson 6532* (CAN); Index Mountain 40 mi. ENE of Arctic Village, 68°15′N, 144°10′W, 11 Jul 1973, *Hettinger 235, 246* (CAN, ALTA); Jago Lake, 69°26′N, 143°47′W, 23 Jul 1957, *Cantlon & Gillis 57-1295* (MSC); King Lodge, Border, Dawson Road, (E of Chicken), 12 Jul 1963, *Spetzman 4883* (CAN); Kodiak, 28 Jul 1904, *Piper 4776* (US); Kogosuknuk River, 69°45′N, 151°45′W, 16 Jul 1953, *Borman, Rebuck & Cantlon 351* (MSC); 69°46′N, 151°40′W, 16 Jul 1953, *Borman, Rebuck & Cantlon 398, 403* (MSC); Kongakut River Hill, 138 mi. NNE of Arctic Village, 69°34′N, 141°50′W, 19 Jul 1973, *Hettinger 347* (CAN, ALTA); Kaness River, 15 mi. SSE of Arctic Village, 67°46′N, 143°45′W, 3 Jul 1973, *Hettinger & Boyce 175 & 176* (ALTA); Kotzebue Sound, 9–16 Aug 1945, *Scamman 3967* (GH); Kotzebue, 12 Aug 1938, *Anderson 4679* (CAS); Big River, 61°55′N, 154°25′W, 10 Jul 1950, *Drury 4211* (GH); Kuskokwim River, Swift River, 62°40′N, 152°30′W, 19 Jul 1961, *Viereck 5067* (CAN); Kenai Peninsula, Steton Creek Valley, 3 Aug 1951, *Calder 6444* (CAS, DAO); Moose Pass, 60°32′N, 149°32′W, 31 Jul 1951, *Calder 6388* (DAO); Knife Ridge, 2 mi. N of Knifeblade, 2 Aug 1951, *Jones 717* (WS); Kokrines Mts., 65°17′N, 154°30′W, 6 Jul 1926, *Porsild 659-60* (CAN, MT, US); Lake Noluk, 2 Aug 1950, *Thompson 1337* (DS, US); Lake Schrader, 69°25′N, 145°00′W, 8 Jul 1948, *Spetzman 529* (DS, US); Lazy Mt., E of Palmer, 29 Jul 1965, *Mitchell 729b6* (DAO); Livengood, 9 Jul 1944, *Anderson 9019* (CAN, MSC); Lodiack, 21 Jul 1904, *Piper 4776* (POM); Mt. McKinley National Park, 2 mi. N of N entrance, 29 Jul 1967, *Hermann 21517* (MICH, NY); Mt. Eielson, Coppers Mt., 11 Jul 1956, *Viereck 1250A* (MIN, RSA); Hines Creek, 6 Aug 1950, *Bailey 5017* (UC); Savage River, 31 Jul 1932, *Henderson 14790* (ORE); Toklat Cabin, 11 Jul 1939, *Murie 35* (RM); Polychrome Pass, mile 43, 1–10 Jul 1964, *Hultén s.n.* (AA); 63°43′N, 149°15′W, 13–22 Jun 1937, *Scamman 585* (GH); Meade River, ca. 15 km from Atkasuk, 70°28′N, 157°25′W, 30 Jun 1966, *DeBenedictis 92, 534* (MICH); milepost 50, along Pipeline Haul Road, 6 Aug 1981, *Allred, Welsh & White 1214* (RSA); Mt. Dustin, 21 mi. from Nome, 4 Jul 1938, *Anderson 3768* (CAS); Nabesna River, 7 Aug 1902, *Schrader & Hartman 67* (US); Nelchina Caribou Range, Tyrone Creek, (100–200 mi. NE of Anchorage), 28 Jun 1957, *Hanson 57-60, 62A, 119* (US); Nome Quad, meadow below radio tower, Anvil Mt., 64°31′N, 165°30′W, 11 Jul 1982, *Kelso 82-39* (COLO); Nome, 1900, *Blaisdell 139* (UC); Ogotoruk Creek, Cape Thompson, 27 Jul 1966, *DeBenedictis 421* (MICH); Okpilak Valley, 69°25′N, 144°02′W, 30 Jun 1958, *Cantlon & Mal-*

*com 58-0117* (MSC); Old John Lake, 27 Jul 1950, *Jordal 3751* (BH, MICH, MT); Pastolik, 5 Jul 1928, *Miller 88c* (US); Port San Juan, Evans Island, 10 Aug 1948, *Eyerdam 7031* (MIN, OSC, RM, WS); Prince of Wales Island, Virginia Mt., 7 mi. S of Pt. Baker, 19 Jul 1972, *Jaques 1476* (OSU); Rapids Lodge, 138 mi. S of Fairbanks on Richardson Hwy., 25–28 Aug 1937, *Scamman 1046* (GH); Seward Peninsula, 64°33′N, 163°45′W, 5–6 Aug 1926, *Porsild & Porsild 1193-94* (CAN, GH); Sheenjek River, 68°22′N, 143°55′W, 19 Jun 1956, *Schaller 54* (MT); Sheenjek River, 68°36′N, 143°45′W, 11 Jun 1956, *Schaller 163* (MT); Snow Camp, Sagavanirkton River, 1958, *Korando & Shanks s.n.* (NY); Sunset Pass, 69°40′N, 144°45′W, 13 Aug 1948, *Spetzman 1154* (CAN, MIN); Tanacross Quad., Sheep Creek, 63°23′N, 143°53′W, 24 May 1977, *Winters 121* (DAO); Taylor Hwy., 64°50′N, 141°15′W, 9 Aug 1965, *Harms 4062* (SASK); Teller, Port Clarence, 6–20 Aug 1949, *Scamman 5433* (GH); Umiat Mt., 2 Jul 1953, *Borman 3394* (MT); 40 mi. NW of Umiat, 29 Jul 1951, *Jones 723* (WS); Umiat, 69°25′N, 152°10′W, 25 Jun 1953, *Bormann, Rebuck & Cantlon 118* (MSC); Upper Marshfork River, 46 mi. NNW of Arctic Village, 68°40′N, 146°30′W, 18 Aug 1973, *Hettinger 814* (ALTA); White River Valley, 61°42′N, 141°39′W, 17 Aug 1968, *Murray 2279* (CAN); Alaska-Yukon Boundary, Firth River and Mancha Creek, 11 Aug 1961, *Stone 1176, 1217* (DS); COLORADO: Park Co., Sheridan Mt., above Hilltop Mine, 12 Jul 1967, *Weber 13299* (COLO); Fairplay, Horseshoe Cirque, T10 R79W S12, 21 Jul 1985, *Dunlop & Orlando 2025* (NHA); South Park, 1873, *Wolfe 1002* (COLO, F, MICH, NY, US); IDAHO: County unknown, Soda Springs, 25 May 1934, *Davis 83-34* (NY); Upper Priest River, 20 Jul 1925, *Epling 7513* (UC); MAINE: Aroostook Co., Aroostook River Basin, 15 Jun 1940, *Chamberlain 1579* (MAINE, UC); Aroostook River, Fort Fairfield, 5 Jun 1901, *Fernald s.n.* (GH, MAINE); Piscataquis Co., Mt. Katahdin, 4 Jul 1856, *Blake s.n.* (MAINE, NHA); North Basin headwall below Hamlin Peak, 1 Aug 1929, *Ewer 226* (MASS); W end of North Basin, 26 Jul 1929, *Ewer 152* (MASS); Chimney Brook, 9 Aug 1926 *Norton, Farring & Rich 17169* (NHA); Chimney Pond, 8 Jul 1900, *Fernald s.n.* (GH, PH); Hawlin Ridge and North Basin, 31 Jul 1923, *Norton, Farring & Rich s.n.* (NHA, USAS, WIS); Trout Brook Mt., T6N R9W, 29 Jul 1946, *Odgen, Chamberlain & Norton 2749* (US); MICHIGAN: Delta Co., Escanaba River, ca. 1 mi. NE of Cornell, ca. 10 mi. NW of Gladstone, 23 Aug 1982, *Voss 15553* (MICH); MINNESOTA: Clay Co., 3 mi. N Downer, 2 Jun 1964, *Stevens 2697* (MIN, UC, US); Audubon Prairie near Moorhead, 23 Jun 1980, *Cross-Leila 167* (MIN); Bluestem prairie near Moorhead, 23 Jun 1980, *Petron 116* (MIN); Polk Co., Pankratz Prairie near Crookston, 18 Jul 1979, *Farrell 117* (MIN); Pembina Trail, 17 Jun 1979, *Sperling 4797* (MIN); Wilkin Co., Barnesville, 17 Jul 1962, *Stevens 2596* (MIN, UC, US); Zimmerman Prairie near Ogema, 26 Jun 1980, *Severson 401* (MIN); MONTANA: Beaverhead Co., Red Rock Pass, 23 Aug 1952, *Booth s.n.* (DAO); Wisdom, 10 Aug 1946, *Booth 1490* (WTU, US); Glacier Co., Cut Bank Pass, 3 Aug 1931, *Cox 643* (US); Hidden Lake Trail, 26 Aug 1962, *Hermann 18300* (MICH, MONTU, US); Logan Pass, 27 Jul 1936, *Pierson s.n.* (CAS); Siyeh Creek, 20 Aug 1985, *Dunlop & Orlando 2256, 2259* (NHA); Lunch Creek, 20 Aug 1985, *Dunlop & Orlando 2264* (NHA); Gunsight Pass, 25 Aug 1919, *Standley 18139* (NY, US); Pigeon Pass, 22 Jul 1958, *Bamberg 92* (COLO); Reynolds Mt., 2 Aug 1960, *Schofield s.n.* (MON-

TU); St. Mary Lake, 6 Aug 1919, *Standley 17150* (US); MacDonald Lake, 3 Aug 1895, *Williams s.n.* (NY, US); Altyn Peak, 13 Jul 1919, *Standley 15596* (NY, US); Divide Mountain, 9 Aug 1964, *Harvey & Pemble 7175* (MONTU, WTU); Teton Co., Pine Butte Preserve, 23 Jun 1982, *Lesica 2055* (MONTU); Antelope Butte, 22 Jul 1982, *Lackschewitz & Ramsden 10049* (COLO, MONTU); Duhr Fen, 16 Aug 1982, *Lesica 2408* (MONTU, WTU); Mt. Patrick Pass, 30 Jul 1983, *Lackschewitz 10609* (MONTU, NY); NEVADA: Elko Co., Ruby Valley, Point Hot Springs, T27N R58E S15, 20 Jun 1984, *Tiehm, Atwood & Williams 8748* (NY, ORE); Ruby Mts., Seitz Lake, T32N R58E S20, 16 Sep 1983, *Goodrich, Smith & Tuhy 20183* (BRY); Ruby Mts., T29N R57E, NW of Harrison Pass, 15 Aug 1980, *Atwood 7713* (BRY); Lamoille Canyon, Thomas Canyon Camp, 15 Jun 1941, *Holmgren 1130* (NY, UC); W of Ruby Mts., along Rt. 229, T32N R60E S19, 4 Aug 1985, *Dunlop & Orlando 2140* (NHA); White Pine Co., Monte Neva Hot Spring, 17 mi. N of McGill, 4 Aug 1985, *Dunlop & Orlando 2130* (NHA); NEW HAMPSHIRE: Carroll Co., Albany, Mt. Chocorua, 4 Jul 1978, *Storks 385* (NHA); Hart's Location, Mt. Willard, Butterwort Flume, 23 Sep 1984, *Dunlop & Orlando 1965-1968* (NHA); Coos Co., Mt. Washington, alpine garden, 31 Jul 1977, *Storks 147* (NHA); Grafton Co., Franconia, Cannon Mt., 4 Aug 1960, *Hodgdon 11670* (NHA); alpine areas of Franconia Mt., *Oakes 3045* (MASS); Mt. Lincoln, summit, 18 Jul 1915, *Fernald & Smiley 11607* (CU, GH, NY, US); Mt. Lafayette, 23 Aug 1865, *Blake* (GH, NHA); Grafton Co., Lyme, on Winslow Ledge, 25 Jun 1984, *Dunlop, Korpi & Hency 2394* (NHA); NEW YORK: Essex Co., N end Indian Pass, 5 Aug 1948, *Smith 4602* (NA); Wilmington, Whiteface Mt., 7 Jul 1986, *Dunlop & Orlando 2414* (NHA); Avalanche Pass, Mt. Marcy, 20 Aug 1924, *Killip 12713* (US); NORTH DAKOTA: Dunn Co., Killdeer Mts., east slope, 11 Aug 1951, *Stevens 1293* (CAN, UC, US); Rolette Co., between Rolette & Thorne, 3 Jun 1913, *Lunell 767236* (MIN, US); OREGON: Wallowa Co., E side Lostine Canyon, 18 mi. above Lostine, 22 Jul 1933, *Peck 17861* (DS, NY, WILLU); Hurricane Creek, 23 Jul 1944, *Peck 22549* (UC, WILLU); Ice Lake meadows, T4S R44E S12, 11 Aug 1961, *Mason 1902* (OSC); UTAH: Duchesne Co., Ashley National Forest, Four Lakes Basin, 22 Aug 1974, *Goodrich 3736* (BRY); Emery Co., Scad Valley, T15S R6E S27, 5 Aug 1984, *Lewis & Lewis 7758* (BRY, UT); Garfield Co., Dixie National Forest, Pine Lake Campground, 31 Jul 1985, *Dunlop & Orlando 2100* (NHA); Upper Henderson Canyon, T35S R1W S32, ca. 11 NE of Tropic, 4 Jul 1983, *Tuhy 863* (RSA); Iron Co., Cedar Breaks, T36S R9W S24, ca. 13 mi. S of Parowan, near Brian Head, 20 Jul 1977, *Welsh & Clark 15512* (BRY, NY); VERMONT: Bennington Co., Mt. Equinox, Deer Knoll, 5 May 1985, *Dunlop, Brackley & Thompson 2003* (NHA); Lamoille Co., Smugglers Notch, Mt. Mansfield, *Pringle s.n.* (CAS, F, GH, MICH, MO, MSC, NHA, NY, PH, POM, UC, VT); Cambridge, in Pringle's Ravine in Smugglers Notch, 4 Aug 1956, *Charette 2288* (VT); Orleans Co., Willoughby Cliffs, 19 Jul 1885, *Deane s.n.* (BH, GH, NY), 25 Jun 1949, *Hodgdon 6046* (NHA); Mt. Pisgah, Lake Willoughby, along Rt. 5A, 16 Aug 1979, *Ahles 78931* (MASS); WYOMING: Johnson Co., Big Horn Mts., 33 mi. NW of Buffalo, T53N R87W S27, 7 Aug 1979, *Nelson 4705* (RM); Park Co., Clay Butte, 15 Aug 1979, *Dorn 3377* (RM); Sheridan Co., Big Horn Mt., T57N R90W S19, 5 Aug 1979, *Nelson 4681* (RM); Tongue River, Aug 1953, *Beetle 6297* (RM); Uinta Co., 5 mi. SW of Hilliard, 25 Jun 1950, *Beetle 11062* (RM).

1b. **Carex scirpoidea** Michx. ssp. **pseudoscirpoidea** (Rydberg) Dunlop, Novon 7: 355. 1997. *Carex pseudoscirpoidea* Rydberg, Mem. N.Y. Bot. Gard. 1: 78. 1900. *Carex scirpoidea* var. *pseudoscirpoidea* (Rydberg) Cronquist, Univ. Wash. Publ. Biol. 17(1): 325. 1969. TYPE: U.S.A. Montana: Spanish Basin, Jul 1896, *Rydberg 3064* (LECTOTYPE: NY! designated by Mackenzie).

Rhizomes elongate, with regularly spaced shoots, internodes 1–2 cm long. Culms usually 1–few per node, arising from shoots of the previous year and retaining the withered, persistent leaf bases of the previous year, scabrous towards apex. Pistillate culms 0.5–1.5 mm wide at top, 0.8–2 mm wide at the base, 5–31 cm tall. Staminate culms 0.9–1.3 mm wide at top, 1.2–2 mm wide at the base, 9–27 cm tall. Leaf sheaths of the rhizome and culm base red-brown to brown-black, glabrous, shiny, becoming fibrous with age. Leaves of the flowering shoots 3–5, clustered, blades diverging from one region up to 20 mm above the culm base, adaxial surface glabrous, scabrous along the margins; in pistillate plants 7–19 cm long, 1.2–3.5 mm wide; in staminate plants 9–12 cm long, 1.5–2.8 mm wide. Vegetative leaves 5–8 per shoot; in pistillate plants 7–21 cm long, 1.6–3 mm wide; in staminate plants 9–13 cm long, 1.5–2.5 mm wide; ligules semicircular, 1–1.4 mm in height, 1.7–3 mm wide. Inflorescences unisexual, unispicate (very rarely with a short sessile lateral spike), erect, linear to oblong, densely flowered; pistillate spikes 10–34 mm long, 3.5–5 mm wide; staminate spikes 10–20 mm long, 3.5–4 mm wide. Involucral bracts often absent, when present foliaceous, shorter than the inflorescence, 6–40 mm long, occasionally scale-like (less than 1 mm and similar to inflorescence scales), inserted on culms 10–47 mm below spike, base occasionally auriculate. Pistillate scales ovate, 2–2.6 (3) mm long, 1.1–1.5 mm wide, longer and wider than the perigynia, apically obtuse, red-brown to brown-black with narrow to wide hyaline margins, central midrib narrow, dark brown not extending to the scale apex; margins ciliate. Staminate scales similar to pistillate, 2.8–4.5 mm long, 0.8–1 mm wide. Perigynia ovate, (1.5) 2–2.8 (3) mm long, 1–1.6 mm wide, abruptly contracted to a beak, lacking a stipe, nerveless, white to light green, becoming red-brown to dark brown towards the apex, hirsute with white to tan hairs; body tightly enveloping the achene; beak 0.1–0.3 mm long, red-brown, straight at maturity, orifice entire and oval. Achenes light brown, 1.5–1.8 mm long, 0.9–1.2 mm wide, lacking a stipe, filling the perigynia or at least ¾ the length and width. Rachilla absent. Anthers 3 mm long.

DISTRIBUTION. *Carex scirpoidea* ssp. *pseudoscirpoidea* is widely distributed in the higher elevations of the western mountains (Figure 2). It is found chiefly in the San Juan Mountains in Colorado; Uinta and La Salle Mountains in Utah; the Sierra Nevada Range in California; Steen Mountains in Oregon; the Sawtooth Range in Idaho; the Little Belts Range, Anaconda-Pintlar Range and Beartooth Plateau in Montana; and the Okanagan Range in eastern Washington and southern British Columbia.

HABITAT. Subspecies *pseudoscirpoidea* occurs at elevations from 3300 to 3900 m, on dry ridge sites and alpine fellfields with gravelly and non-calcareous soils.

Subspecies *pseudoscirpoidea* is distinct ecologically, occurring chiefly in high elevation sites in mountain ranges in the West. This taxon is distinguished by culms that arise from second year shoots, clothed at the base by the withered and persistent leaf bases of the previous year. Generally, a single culm arises from a node and internodes of the rhizome are elongated, typically 1–2 cm. The leaves are clustered, diverging from the shoot axis at one point approximately 10–20 mm above the rhizome, in contrast to other taxa in which the leaves diverge from the stem at scattered intervals along the shoot axis. The plants generally have shorter and wider leaves than those of ssp. *scirpoidea.*

In lectotypifying *Carex pseudoscirpoidea,* Mackenzie (1935) chose *Rydberg 3064* (NY) as the lectotype. Unfortunately, this is a staminate plant and does not possess some of the diagnostic features of the taxon.

REPRESENTATIVE SPECIMENS: **Canada.** BRITISH COLUMBIA: Cathedral Ridge, ca. 4½ mi. N of Monument 95, 28 Aug 1972, *Douglas & Douglas 4629* (ALA); Cathedral Park, Lake Lady Slipper, 12 Jul 1975, *Hainault 7728* (DAO), 14 Jul 1975, *Hainault 7526* (DAO); Lakeview ridge, 28 Jul 1976, *Hainault 7962* (DAO); Mt. Apex, 11 Aug 1964, *McLean & Haupt 65-64* (DAO), *McLean & Marchand 65-63* (DAO); Mt. Bomford, Cathedral Lakes, Ashnolda District, 49°N, 120°15′W, 11 Jul 1951, *Taylor 1359* (UBC).

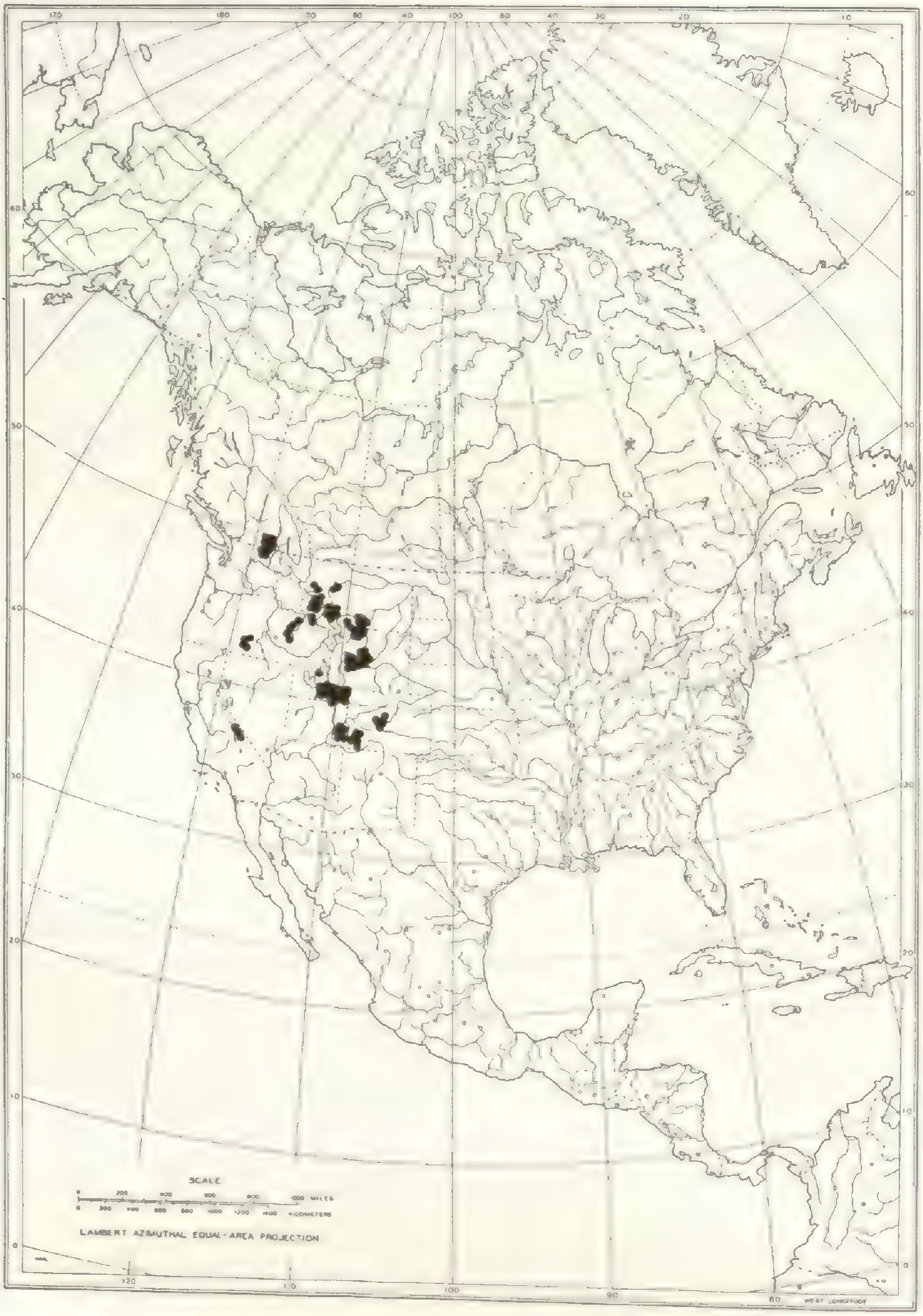
SCALE
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
WEST LONGITUDE

Figure 2. Distribution of *Carex scirpoidea* ssp. *pseudoscirpoidea.*

**United States.** CALIFORNIA: Alpine Co., Carson Pass, Round Top Lake to Fourth of July Lake, 29 Aug 1974, *Taylor 4910* (DAV); Mono Co., Minarets Wilderness Area, Inyo National Forest, Dana Plateau, N of Mt. Dana, T1N R25E S28, 7 Aug 1985, *Dunlop & Orlando 2158* (NHA); COLORADO: Chaffee Co., Monarch Pass, 20 mi. W of Salida, 22 Jun 1926, *Erlanson 2020* (MICH); Manassas Creek, 24 Jul 1919, *Clokey 3337* (BH, MO, NY, RM, UC, US); Gunnison Co., North Pole Basin, 14 Jul 1955, *Weber & Barclay 9193* (COLO, CS, DS, MT, NY, RM, RSA, UC); La Plata Co., San Juan National Forest, Chicago Basin, Eoleus, 29 Jul 1962, *Michener 724* (COLO); San Juan Co., San Juan National Forest, Eldorado Lake, T40N R6W, 19 Jul 1971, *Instarr s.n.* (COLO); San Juan National Forest, NoName Basin on Middle Ridge, 6 Aug 1962, *Michener 750a* (COLO); IDAHO: Blaine Co., Sawtooth Range, Devil's Bedstead, 28 Jul 1936, *Thompson 13562* (CAS, CU, PH, MO, NY, WS, WTU); Sawtooth National Forest, head Boulder Creek, 4 Aug 1937, *Thompson 14114 ½* (CAS, WTU); MONTANA: Beaverhead Co., Oreamnos Lake, 25 Jul 1945, *Hitchcock & Muhlick 12793* (BH, CAS, PH, NY, WS, WTU); Pioneer Range, Black Lion Mountain, 30 Jul 1945, *Hitchcock & Muhlick 12977* (BH, CAS, NY, WS, WTU); Torrey Lake, 27 Jul 1946, *Hitchcock & Muhlick 15050* (CAS); Carbon Co., Moon Lake, 15 Aug 1979, *Lackschewitz 9154* (MONTU); Beartooth Mountains near Wyoming state line, 25 mi. SW of Red Lodge, T9S R19E S32, 22 Jul 1955, *Cronquist 7998* (CAN, CAS, CU, DAO, DS, GH, MICH, MONTU, MT, NY, OSC, RM, RSA, UC, WTU); Hell Roaring Plateau, 25 Jul 1921, *Simms & Zeh 640* (RM); Deerlodge Co., Mt. Tiny above Goat Flats, 10 Sep 1972, *Lackschewitz 4123* (MONTU); Deerlodge National Forest, meadow below Storm Lake Pass, T4N R13W S30 & 31, 24 Aug 1985, *Dunlop & Orlando 2280* (NHA); Anaconda Pintlar Wilderness, T3N R14W S36, SW of Mt. Tiny on Storm Lake trail to Goat Flats, 24 Aug 1985, *Dunlop & Orlando 2285* (NHA); Madison Co., Gravelly Range, Black Butte, 26 Jul 1947, *Hitchcock 16869* (CAS, NY, RSA, WS); Tobacco Root Mts., Mt. Bradley, 26 Aug 1959, *Bamberg 431* (COLO); Taylor Mts., Koch Peak, 2 Aug 1946, *Hitchcock & Muhlick 15194* (CAS, MO, NY, WS, WTU); Missoula Co., Bitterroot Mts., Lolo Peak, 8 Sep 1968, *Lackschewitz & Fageraas 1081 a&b* (MONTU); OREGON: Harney Co., Steen Mts., above Alberson, 5 Jul 1925, *Peck 14272* (CAS, F, PH, WILLU); Big Indian Gorge, T33S R33E S35, 28 Aug 1980, *Wright 1468* (OSC); UTAH: Daggett Co., Leidy Peak, 31 Jul 1929, *Dremolski D-7* (RM); Duchesne Co., Atwood Lake, 28 Jul 1945, *Hayward 39, 40* (BRY); Mt. Emmons, Chain Lakes, Kregs Basin, 18 Jul 1933, *Hermann 4935* (CAS, DS, MICH, MO, NY); Garfield Basin, Bluebell Lake, T4N R5W S31 & 32, 30 Jul 1980, *Neese & Welsh 214016* (NY); Uinta Mts. N slope 1 mi. SE of Island Lake, 25 Sep 1983, *Neely & Carpenter 1892* (COLO); West Granddaddy Mtn., T2N R8W S7, 5 Sep 1984, *Tuhy 2226* (BRY); Yellowstone Canyon, Milk Lake, T4N R5W S25, 2 Aug 1980, *Welsh & Neese 213930* (NY); San Juan Co., La Sal Mountains, W end Dark Canyon, Mt. Peale, T27S R24E S13, 26 Jul 1985, *Dunlop, Orlando & Franklin 2075* (NHA); Mt. Mellenthin, T27S R24E S12, 26 Jul 1984, *Tuhy 1746* (BRY); Summit Co., Bald Mt. summit, 3 Sep 1953, *Lewis 267* (BRY, CAS); near divide W of Fish Lake on N slopes of Uinta Mts., T2N R11E S2, 3 Sep 1945, *Harrison & Harrison 10971* (BRY, US); rocky washes above Dollar Lake, Henry's Forks Basin, 12 Aug 1936, *Maguire, Hobson & Maguire 14580* (CAS, DAO, RM, US, WS, WTU); Lamotte Peak, streamlet below lake, 15 Aug 1933, *Hermann 5971* (RM, MICH, MO); Uinta Co., Uinta Mts., Ashley National Forest, 22 mi. NW of Vernal, T15 R19E S27, 2 mi. E of Marsh Peak, 19 Aug 1982, *Goodrich 17689* (BRY, UT); 2 mi. NW of Paradise Park Res., T3N R1W S2, 5 Jul 1980, *Goodrich 14253* (BRY); E side Leidy Peak, T1N R19E S31, 24 Jul 1986, *Goodrich 22074* (BRY); East Fox Lake, Uinta River, 14 Aug 1953, *Lewis 230* (BRY); WASHINGTON: Okanogan Co., Chopaka Mt. ca. 11.5 mi. NW of Loomis, 16 Jul 1972, *Douglas & Douglas 3858* (DAO); Tiffany Lake Pass, 24 Jul 1931, *Fiker 406* (WILLU, WS); Windy Peak, ca. 17 mi. NW of Loomis, 17 Aug 1971, *Douglas 3120* (RM); WYOMING: Fremont Co., Shoshone National Forest, East Fork Wind River, 8 Aug 1962, *Johnson 249, 250* (CS, RM); Wind River Range, Roaring Fork Mt., 2 mi. NW of Silas Lake, 20–26 Jul 1965, *Scott 535* (CAN, GH, UC); Johnson Co., Big Horn Forest, Grasshopper Ridge, Elk Lake, 28 Aug 1961, *Johnson 144* (RM); Park Co., Island Lake, 19 Jul 1948, *Daubenmire 48330* (WS); Little Bear Creek, cross Hwy. 212, 17 Jul 1973, *Taylor 1606* (RM); Sublette Co., Bridger National Forest, Bridger Wilderness Area, near Lake Timeco, 5 Aug 1976, *Beetle 16673* (RM); White Rock Mt., near Green River Lakes, 8 Aug 1925, *Payson & Payson 4605* (MO, MSC, NY, PH, RM, WS).

1c. **Carex scirpoidea** ssp. **convoluta** (Kükenthal) Dunlop, Novon 7: 355. 1997. *C. scirpoidea* var. *convoluta* Kükenthal, in Engler, Das Pflanzenreich 38 (IV:20): 81. 1909. TYPE: U.S.A. Michigan: Thunder Bay Island, 18 Aug 1895, *Wheeler s.n.* (HOLOTYPE: B destroyed; ISOTYPES: BH! CAN! GH! MICH! MIN! MSC! NY! POM! VT!).

Rhizomes short. Culms one to several per node, arising from current year shoots (lacking any withered persistent leaf bases of the previous year), scabrous especially at the apex. Pistillate culms 0.4–0.7 mm wide at the top, 0.8–2.2 mm wide at the base, (9.2) 19.5–35 (38) cm tall. Staminate culms 0.5–0.9 mm at the top, 0.9–1 mm wide at the base, 9–31 cm tall. Leaf sheaths of the rhizome and the culm base red-brown to brown-black, glabrous, shiny, coriaceous with acute hard tips. Leaves of the flowering shoots 2–4, not clustered, adaxial surface glabrous, margins scabrous; in pistillate plants 7–18 cm long, (0.8) 1.1–1.5 (2) mm wide; in staminate plants 6–15 cm long, 1–1.5 wide. Vegetative leaves 4–9 per shoot; in pistillate plants 10.5–23.4 cm long, (0.7) 1–2 mm wide; in staminate plants 11–16 cm long, 1–1.7 mm wide; ligules semicircular, 0.2–2 (3) mm in height, 1–2 mm wide. Inflorescences unisexual, unispicate (very rarely with a short lateral, sessile or subsessile spike), erect, linear, densely flowered; pistillate spikes slender, (10.6) 15–21 (30) mm long, 2.5–3.5 (4) mm wide; staminate spikes 13–30 mm long, 2–3.5 mm wide. Involucral bract usually absent, when present foliaceous, shorter than the inflorescence, 5–21 mm long, base inserted on culm 5–12 mm below spike, auriculate. Pistillate scales ovate to obovate, (1.5) 2–2.4 mm long, (0.9) 1–1.2 mm wide, equal to or shorter than perigynia, apex obtuse to acute, red-brown to dark brown with narrow to broad hyaline margins, central midrib narrow green-tawny to dark brown, extending to scale apex; margins entire. Staminate scales similar to pistillate, 2.5–3.2 mm long, 0.7–0.9 mm wide. Perigynia ovate to obovate, 1.5–2.6 mm long, (0.7) 1–1.2 mm wide, as wide as the subtending scale, abruptly contracted to a beak, lacking a stipe, nerves absent, basally light green, becoming tawny to red-brown towards apex, hirsute with white to tan hairs, body tightly enveloping the achene; beak 0.1 mm long, red-brown and hyaline at tip, straight at maturity, orifice entire and circular. Achenes dark brown, 1–1.5 mm long, 0.6–0.9 mm wide, sessile or with 0.25 mm stipe, filling the perigynia or at least ¾ the length and width. Rachilla absent. Anthers 1.5–2 mm long.

DISTRIBUTION. This is the most geographically restricted of the four subspecies (Figure 3), occurring only along the shores of Lake Huron on the Bruce Peninsula, on islands of the Manitoulin District, Ontario, and on Drummond Island and Thunder Bay Island, Michigan.

HABITAT. Subspecies *convoluta* is associated with alvar communities, characterized by Catling and Brownell (1995) and Stephenson (1983), as areas with sparse vegetation and thin soil over flat limestone or marble substrate. These open alvar communities contain a number of plant species that are calcicolous, often drought resistant, and grow in cracks of outcropped limestone "pavements."

Subspecies *convoluta* is distinguished by narrow, convolute leaves of the vegetative and flowering shoots, a strongly cespitose habit, and a higher number of flowering culms per plant than other subspecies.

These narrow-leaves plants were first described as a variety of *Carex scirpoidea* by Kükenthal based on specimens collected by Wheeler in 1895 from Thunder Bay Island, Michigan. Unfortunately, Kükenthal's *Carex* herbarium, presumably including the holotype of *C. scirpoidea* var. *convoluta,* was sent to Berlin (B) and was destroyed during World War II (Stafleu and Cowan 1979). Isotypes of Wheeler's 1895, Thunder Bay Island, Michigan, collections are available.

REPRESENTATIVE SPECIMENS: **Canada.** ONTARIO: Algoma District, Great Cloche Island, 26 Jul 1956, *Soper & Fleischmann 6633* (CAN); Bruce Co.,

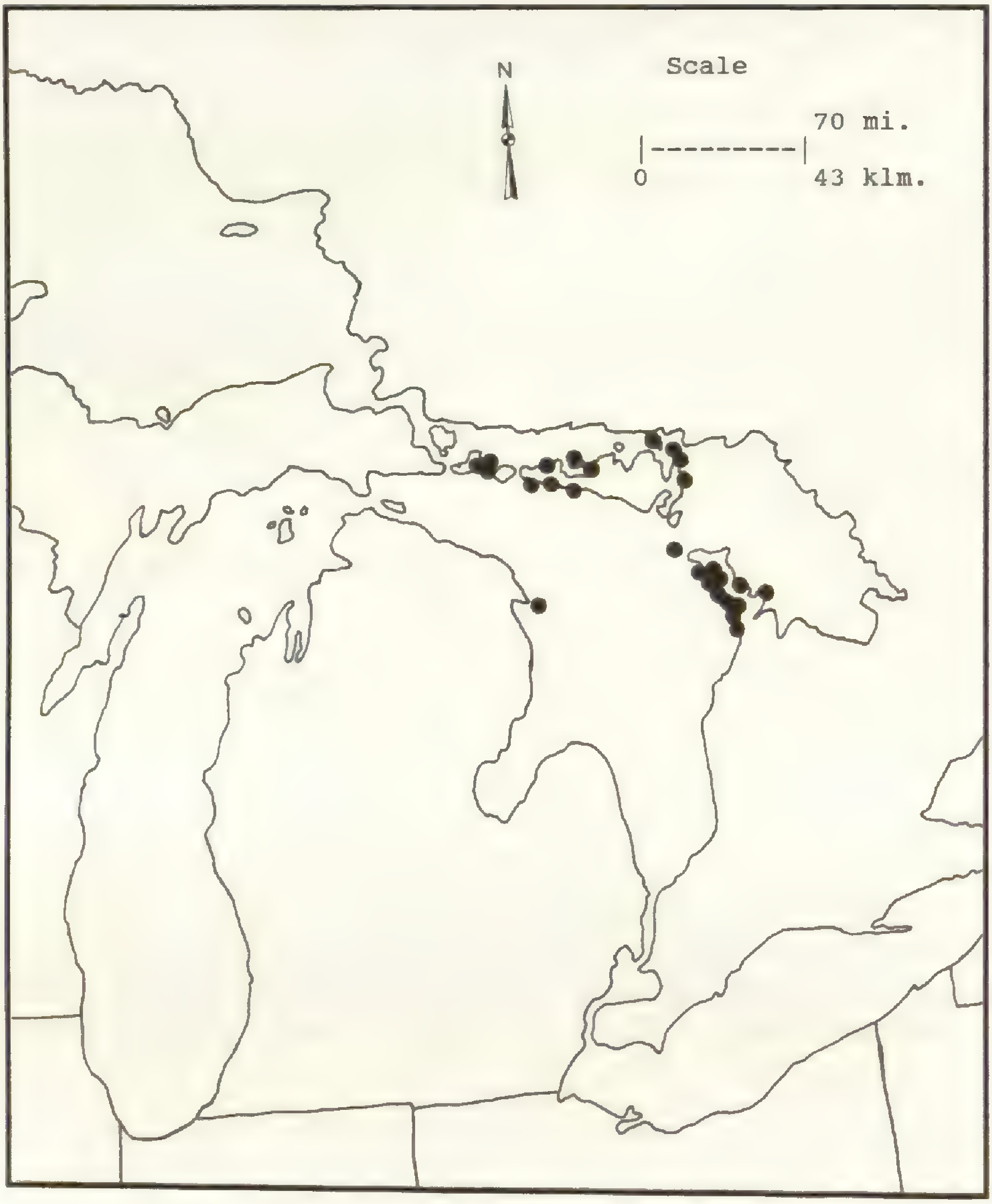

Figure 3. Distribution of *Carex scirpoidea* ssp. *convoluta.*

Cape Croker, MacGregor Harbour, 19 May 1969, *Morton 2658* (CAN, WAT); Dorcas Bay, 2 Jun 1979, *Webber s.n.* (TRTE), 23 Jun 1971, *Masih & Keal 579* (TRTE); French Bay, 22 Aug 1898, *Dearness 2518* (DAO); between Frenchman Bay and Sauble Beach South, 3 Jun 1950, *Soper & Shields 4538* (CAN, DAO, MO, MT); Howdenvale, 31 Jul 1936, *Watson 2904* (CU, NY, US); Lion's Head, 11 Jun 1932, *Marie-Victorin, Rousseau & Prat 45-922* (DAO, GH, MT); Little Pine Tree Harbour, Zinker Island Cove, 30 Jun 1982, *Webber 4552* (TRTE); Oliphant, 9 Aug 1971, *Montgomery 3693* (WAT); Red Bay, 9 Jul 1941, *Sargent 5* (GH); Sauble Beach, 20 Jun 1934, *Taylor & Fernald s.n.* (WIS); Stokes Bay, 26 May 1934, *Krotkov 8759* (NY, US), *8792* (GH); Barrie Island, May 1979, *Hogg s.n.* (CAN, WAT); Georgian Bay Island National Park, Cove

Island, Bass Bay, 22 Sep 1981, *Bobbette 7403* (WAT); Zinkan Island, 45°04′N, 81°29′W, 15 Jul 1975, *Cuddy & Emalie 1815* (CAN); Manitoulin District, Barrie Island, Rozels Bay, 29 Jul 1985, *Hellquist 15513* (NASC); Green Island Harbour, 20 Jul 1976, *Ringius & Wilson 327* (WAT); Hensly Bay, 26 May 1978, *Morton & Venn 11521* (WAT); La Cloche Peninsula, 20 Aug 1932, *Fassett 14899* (WIS, GH), 11 Jul 1957, *Pease & Bean 26203* (GH); Whitefish River W side Hwy. 68, 3 Jul 1976, *Catling & McIntosh s.n.* (DAO, WIS); Misery Bay, 28 Jul 1972, *MacDonald & White 3593* (CAN); Murphy Point, 14 Jul 1952, *Senn 5974* (DAO, MT, NY, PAC, US, WS); Tamarack Cove, 20 Jul 1932, *Koelz 4206* (MICH, WIS); Tamarack Point, *Grassl 4594* (MICH).

**United States.** MICHIGAN: Alpena Co., Thunder Bay Island, 18 Aug 1895, *Wheeler s.n.* (BH, CAN, GH, MICH, MIN, MSC, NY, POM, VT); Chippewa Co., Drummond Island, Meade Island, 19 Jun 1979, *Voss 15074* (MICH).

1d. **Carex scirpoidea** Michx. ssp. **stenochlaena** (Holm) Löve and Löve, Taxon 13: 202. 1964. *C. scirpoidea* Michx. var. *stenochlaena* Holm, Amer. J. Sci. IV 18: 20. 1904. *C. stenochlaena* (Holm) Mackenzie, Bull. Torrey Bot. Club 35: 269. 1908. TYPE: CANADA. British Columbia: Chilliwack Lake, by a rivulet, 4000 ft., 12 Jul 1901, *Macoun 33728* (LECTOTYPE: CAN 21326! designated herein; ISOLECTOTYPES: CAN! MO! MSC! NY! US!).

Rhizomes short. Culms several per node, arising from shoots of the current year, (lacking any withered persistent leaf bases of the previous year), scabrous toward the apex. Pistillate culms 0.6–1 mm wide at the top, 1.4–2.1 mm wide at base, 24–34 cm tall. Staminate culms 0.5–0.8 mm wide at the top, 2.2–3 mm wide at the base, 14–26 cm tall. Leaf sheaths of the rhizome and the culm base red-brown to brown-black, glabrous, shiny, coriaceous. Leaves of the flowering shoot 3–5, not clustered, adaxial surface glabrous, margins scabrous; in pistillate plants 12.5–25 cm long, 1.4–2.1 mm wide; in staminate plants 14–20 cm long, 1.5–2.4 mm wide. Vegetative leaves 5–6 per shoot; in pistillate plants 10–28 cm long, 1–2.5 mm wide, in staminate plants 19–24 cm long, 1.4–2.5 mm wide; ligules semicircular, 0.8–1.5 mm in height, 1–2.5 mm wide. Inflorescences unisexual, unispicate (occasionally with a single, short lateral spike), drooping on lax culms, mostly clavate, loosely-flowered especially at base; pistillate spikes 25–30 mm long, 3.5–6.5 mm wide; staminate spikes (few seen) 18–25 mm long, 4–5 mm wide. Involucral bract single, foliaceous, shorter than the inflorescence, 4–40 mm long, base inserted on culms 10–33 mm below spike, auriculate. Pistillate scales oblong-lanceolate, 2.4–3.5 mm long, 1–1.5 mm wide, equal to or shorter than perigynia, apex subacute to acute, red-brown to black, without hyaline margins; central midrib obscure, only slightly raised, red-brown, but lighter in color than rest of scale, extending to the apex; margins ciliate. Staminate scales similar to pistillate, (3.5) 4.5–5 (6) mm long, (0.7) 1–1.4 mm wide. Perigynia lanceolate to oblanceolate, (2.8) 3–4 (5) mm long, 0.9–1.4 (1.6) mm wide, as wide as subtending scale, tapering gradually to beak, with short basal stipe, adaxial surface nerveless or with few short obscure basal nerves, red-brown to black, rarely tan, hirsute with tan to brown hairs, loosely enveloping the achene in upper ⅓; beak 0.3–0.5 mm long, dark brown and not hyaline, reflexed at maturity, orifice entire and abaxially oblique. Achenes light brown, 1.2–2 mm long, 0.8–1 mm wide, with 0.25–0.50 mm stipe, filling ½ to ⅔ the length of the perigynia. Rachilla absent. Anthers 3–3.5 mm long.

DISTRIBUTION. This subspecies occurs in the Cascade Mountains in Washington, the Bitterroot Mountains in Montana, the coastal ranges in southern British Columbia, and at a few localities in Alaska and the Yukon (Figure 4).

HABITAT. In the Bitterroot Mountains of Ravalli County, Montana, this subspecies grows on bedrock terraces between 1615–2620 m elevation, especially between 2130–2440 m. In Washington it grows mostly between 1460–2010 m.

This taxon is associated with weakly acidic soils which have high levels of magnesium and low levels of calcium. Edaphic requirements may be an important isolating factor for this subspecies. More detailed studies of habitat requirements and microenvironments are required before one can speculate on the history of this taxon and how it is related to the other subspecies.

Subspecies *stenochlaena* is distinguished by lanceolate perigynia which are greater than 3 mm long, taper gradually to a beak, and are over 2.5 times as long as wide. The pistillate spikes are clavate, loosely flowered at the base, and borne on slender, lax culms which cause the spikes to droop. The pistillate scales are over 3 mm long, subtending hirsute perigynia with tan, yellow, or golden-brown hairs. Both perigynia and pistillate scales are dark brown to black. Beaks are dark and reflexed at maturity, with an oblique mouth.

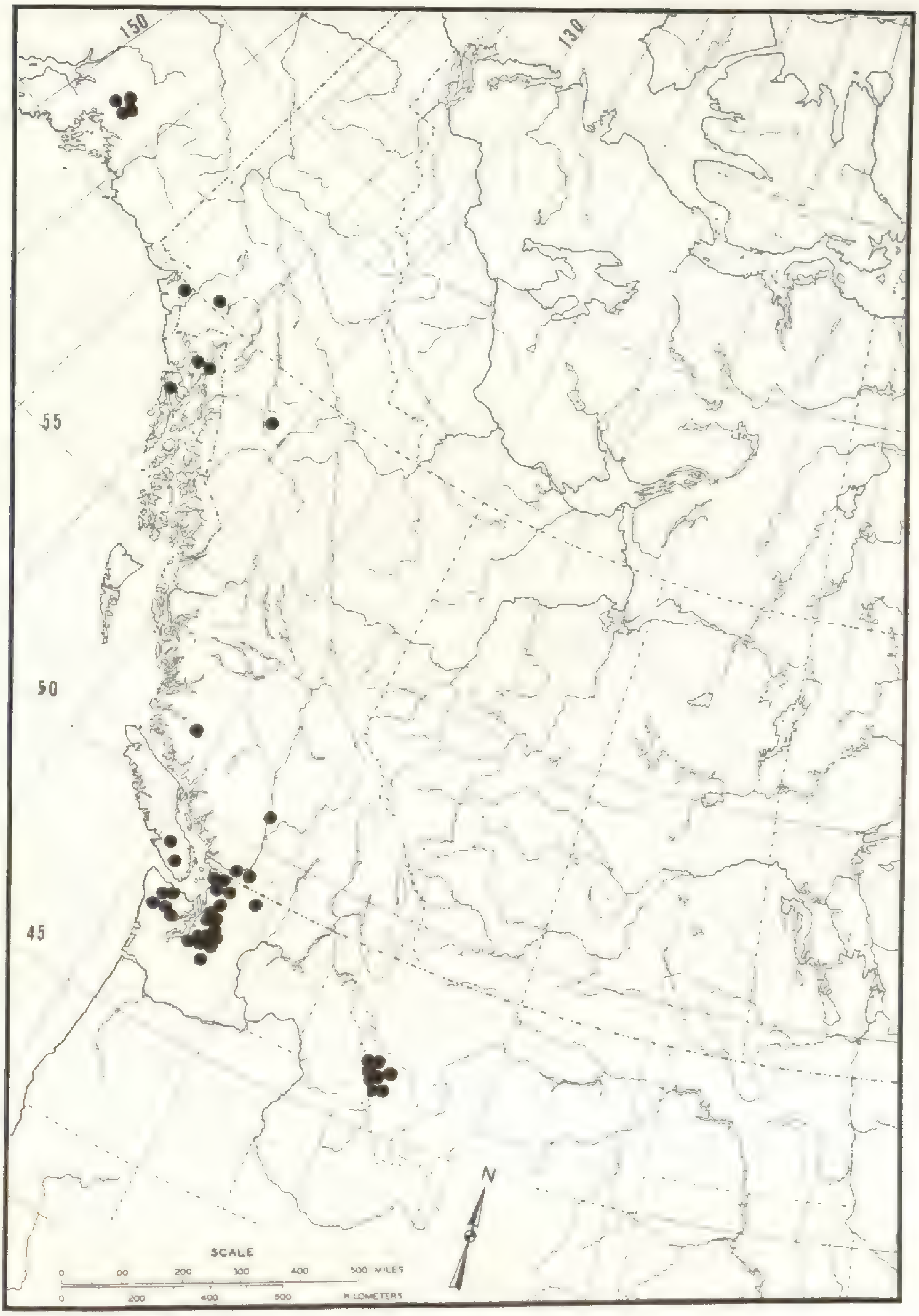
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Figure 4. Distribution of *Carex scirpoidea* ssp. *stenochlaena*.

A lectotype, designated herein, has been selected from Macoun's specimens since no specimen was chosen by Holm. The lectotype (CAN 21326) is a Macoun specimen bearing a "Geologic Survey of Canada" label, while others bear "Ex. Herb. Geologic

Survey of Canada" labels. The latter are isolectotypes bearing the same number as the lectotype, but having a slightly different wording of the locality data.

Some geographically based variation is present within this subspecies. Specimens from Washington and the Bitterroot Range in Ravalli County, Montana have the longest perigynia, often reaching 4.3 mm, and are the most distinct from ssp. *scirpoidea.* Specimens from Alaska, northern British Columbia and the Yukon exhibit tendencies towards ssp. *scirpoidea.* Fifteen percent of these plants have perigynia just under 3 mm long (high end of ssp. *scirpoidea* range) and perigynia length-to-width ratios over 2.5 (unlike those of ssp. *scirpoidea* which are less than 2.5 times as long as wide); they lack the clavate, loosely flowered spikes characteristic of plants of ssp. *stenochlaena* in Washington and Ravalli County, Montana. The intergradation observed in plants from British Columbia and elsewhere might be the result of hybridization between ssp. *stenochlaena* and ssp. *scirpoidea* at localities where their ranges overlap. For this reason, subspecies *stenochlaena* is recognized at the subspecific level, rather than the specific level.

REPRESENTATIVE SPECIMENS: **Canada.** BRITISH COLUMBIA: Bluster Mt., Marble Mts., 14 Jul 1938, *Thompson & Thompson 455* (CAS, DAO, F, GH, MO, NY, US, WTU); Chilliwack Valley, 49°10′N, 121°–122°25′W, 12 Jul 1901, *Macoun 33728* (CAN, MO, MSC, NY, US); Katherine Lake, 57°26′N, 126°48′W, 25 Jul 1977, *Gillett & Boudreau 17441* (CAN); Kinbasket, Big Bend Hwy., Sullivan River, 1 Aug 1947, *Eastman 15994* (DAO, UBC); Maroon Mt., 54°47′N, 128°40′W, 18 Sep 1977, *Foster 9* (UBC); McGillivray Creek, Cascade Range, 10 Aug 1916, *Macoun 97965* (CAN, GH, US); Moose River, 15–17 Jul 1911, *Hollister 43* (NY, US); Mt. Assiniboine Park, Lake Magog, 16 Jul 1937, *Rose 37550* (CAS, UC); Mt. Chelam, 15 Aug 1901, *Anderson s.n.* (MO); Noaxe Lake, 4 Aug 1957, *Brink s.n.* (DAO, OSU, UBC); Ellis Point & Mercer Point, W of Skidegate channel, Graham Island, *Calder & Savile 22870* (DAO, DS, GH, NY, RSA, UC, WS, WTU); Vancouver Island, Marble River, N of Alice Lake, 13 Jul 1964, *Hett & Armstrong 403* (DAO); Marble Lake, near Jeune Landing, 13 Jul 1964, *Hett & Armstrong 399* (DAO); Mt. Klitsa, 22 Jul 1971, *Pojar 177* (UBC); YUKON TERRITORY: Alsek Valley, ca. 8 mi. W of Mackintosh, 5 Jul 1957, *Schofield & Crum 7559* (DS, UBC); Canol Road, mile 132, Lower Lapie River, 26 Jun 1944, *Porsild & Breitung s.n.* (NY, US), 22 Jun 1944, *Porsild & Breitung 11981* (CAN); Canol Road, Mt. Sheldon, 3 Aug 1944, *Porsild & Breitung 11708* (CAN), *11703* (GH); Kluane Lake, near Rusty Glacier, W of Burwash Landing, 61°16′N, 140°15′W, 9 Jul 1968, *Murray 1671* (CAN); Mackintosh, mile 1002, Alaska Hwy., Alsek Valley Road, 4–5 Jul 1957, *Schofield & Crum 7520, 7560, 7561* (CAN).

**United States.** ALASKA: Charlie River, 64°50′N, 143°40′W, 30 Aug 1956, *Argus 872* (RM, SASK); Chugach Range, Tazalina Glacier, 61°45′N, 146°30′W, 19 Jul 1957, *Viereck 2194* (CAN); Juneau, 10 Jul 1917, *Anderson 365* (NY); Mt. McKinley National Park, 2 mi. N of N entrance, 29 Jul 1967, *Hermann 21517* (MICH, NY); Wonder Lake, *Argus 660* (SASK); Mt. Hayes, *Palmer 606* (US); Mt. Roberts, Juneau, 26 Jun 1925, *Anderson 2A233* (GH); Yes Bay, 16 Jul 1895, *Howell 1705* (CAS, MSC, NY, US); MONTANA: Ravalli Co., Bitterroot National Forest, Bailey Lake, 22 Aug 1985, *Dunlop & Orlando 2272* (NHA); Bitterroot-Selway Divide above Baily Lake, 12 Jul 1969, *Lackschewitz 1344* (NY, RM); Chaffin Lake Basin, Chaffin Peak, 30 Aug 1971, *Lackschewitz 3397* (MONTU); Sheafman Lake, 17 Aug 1979, *Lackschewitz 2317* (MONTU); St. Joseph's Peak, 31 Jul 1969, *Lackschewitz & Fageraas 1631* (MONTU); Tin Cup Lake, 19 Jun 1971, *Lackschewitz 2727* (MONTU); Trappers Peak, 14 Aug 1946, *Hitchcock & Muhlick 15381* (CAS, NY, WTU); White Mt., 11 Aug 1970, *Lackschewitz & Smith 2277* (MONTU); WASHINGTON: Chelan Co., Crown Point, Holden-Lyman Lake Trail, 20 Aug 1956, *Raven 10176* (CAS); Ingalls Peak, 20 Jul 1925, *St. John & Thayer 7239* (WS); Mt. Stuart, 23 Jul 1933, *Thompson 9580* (DS, GH, MO, NY, RSA, UC, US, WTU); Skagit Pass, 24 Aug 1892, *Lake & Hull 408* (WS); Clallam Co., Mt. Angles, Starvation Flats, 17 Jul 1931, *Thompson 7419* (PH, WTU); Olympic Mt., Aug 1895, *Piper 2243* (BH, GH, WS); Jefferson Co., Mt. Anderson, 28 Jul 1936, *Meyer 686* (MO, WS); King Co., Denny Creek, 19 Aug 1936, *Thompson 13684* (CAS, MO, NY, PH, WS, WTU); Guy Peak, Snoqualmie Pass, 7 Aug 1933, *Thompson 9690* (NY, WTU); Kittitas Co., Beverly Creek Trail, T22N R15E ca. S1, 17 Aug 1985, *Dunlop & Orlando 2241* (NHA); Fish Lake, 17 Jun 1934, *Thompson 10663-4* (CAS, DS, GH, NY, POM, US, WTU, UWT); Okanogan Co., Hart's Pass, ca. 20 mi. E of Diablo, 11 Jul 1971, *Douglas 2866* (ALTA); Horse Shoe Basin, Sep 1897, *Elmer 684* (MIN, MO, NY, POM, US, VT, WS); Snohomish Co., Mt. Pugh, 18 Aug 1938, *Thompson 14340* (CAS, GH, WTU); Whatcom Co., Crater Mt., 20 Aug 1971, *Naas 1240* (RM); Twin Lakes, Jackson Mt., 7 Sep 1927, *St. John 8941* (WS, RM); Mt. Shuksan, ca. 22 mi. N of Rockport, 13 Jul 1969, *Douglas 1417* (RM).

2. **Carex curatorum** Stacey, Leafl. W. Bot. 2: 13. 1937. *C. scirpoidea* var. *curatorum* (Stacey) Cronquist, Intermountain Flora 6: 113. 1977. Type: U.S.A. Arizona: Grand Canyon National Park, Kaibab Trail to Roaring Springs, 23 Jun 1933, *Eastwood & Howell 1100* (LECTOTYPE: CAS 204972! designated herein).

*Carex haysii* Welsh, Mem. N. Y. Bot. Gard. 64: 124. 1990. Type: U.S.A. Utah: Washington Co., Zion Canyon, Lower Emerald Pool, Springdale Sandstone, hanging garden, sandy bank and cliff face, ca. 4300 ft. T41S R10W S9, 5 Jun 1989, *Welsh, Clark & Hays 24335* (HOLOTYPE: BRY; ISOTYPES: CAS, MICH!, NY!, POM, RM, UT).

Rhizomes short and forming mats. Culms one to several per node, arising from current year shoots (lacking the withered persistent leaf bases of the previous year), strongly scabrous the full length of culm. Pistillate culms 0.4–1.2 mm wide at the top, 0.7–3.5 mm wide at the base, (23) 35–91 cm tall. Staminate culms

0.5–1 mm wide at the top, 0.9–4.5 mm wide at the base, 20–74 cm tall. Leaf sheaths of the rhizome and culm bases light brown to purple-black, glabrous, dull, coriaceous. Leaves of the flowering shoots 2–6, arising from the base and not clustered, adaxial surface sparsely pilose especially along median adaxial groove and veins, margins strongly scabrous; in pistillate plants 12–57 cm long, 1.5–2.3 mm wide; in staminate plants 12–25 cm long and 1.2–3.1 mm wide. Vegetative leaves 4–11 per shoot; in pistillate plants 14–55 (79) cm long, 1.1–2.3 mm wide; in staminate plants 18–55 cm long, 1.2–1.9 mm wide; ligules triangular, 1.4–4.2 (5) mm in height, 1.1–2.3 mm wide. Inflorescences unisexual (rarely bisexual), not strictly unispicate, (occasionally with 1–2 short lateral spikes of the same sex in the axil of the involucral bract or subtending the terminal spike), erect or drooping on lax culms, linear, loosely to densely flowered; pistillate spikes 17–43 mm long, 2.5–5 mm wide, staminate spikes 13–37 mm long, 2–5 mm wide. Involucral bract usually present, usually single, foliaceous or scale-like, shorter than or equal to length of the inflorescence, 6–11 cm long, base inserted 5–75 mm below spike, auriculate. Pistillate scales oblong-lanceolate, 2–3.5 mm long, 0.7–1.9 mm wide, half as long as to equaling the perigynia, apically acute, red-brown with narrow to broad hyaline margins; central midrib narrow, extending to apex, occasionally prolonged into a short awn; margins entire, sometimes ciliate. Staminate scales similar to pistillate, 3.5–4.3 mm long, 1–1.3 mm wide. Perigynia obovate to ovate, 2–3 (4) mm long, 1.5–1.8 mm wide, wider than subtending scale, tapering gradually or abruptly contracted to a beak, with few obscure nerves on the adaxial surface over the achene, marginal nerves evident, pale green to tawny becoming red-brown towards apex, hirsute with white hairs; body not tightly enveloping the achene; beak 0.1–0.5 mm long, red-brown and hyaline at tip, straight at maturity, orifice entire and adaxially oblique. Achenes dark brown, 1.2–2 mm long, 0.8–1.2 mm wide, stipe 0.25 mm, filling only ⅓–½ the length of the perigynia and ⅓ the width such that the perigynia sides are compressed and contracted at the base. Rachilla often present. Anthers 1.7–2.4 mm long.

DISTRIBUTION. *Carex curatorum* is limited to southern Utah and adjacent northern Arizona (Figure 5), especially along the Colorado and San Juan Rivers and their tributaries.

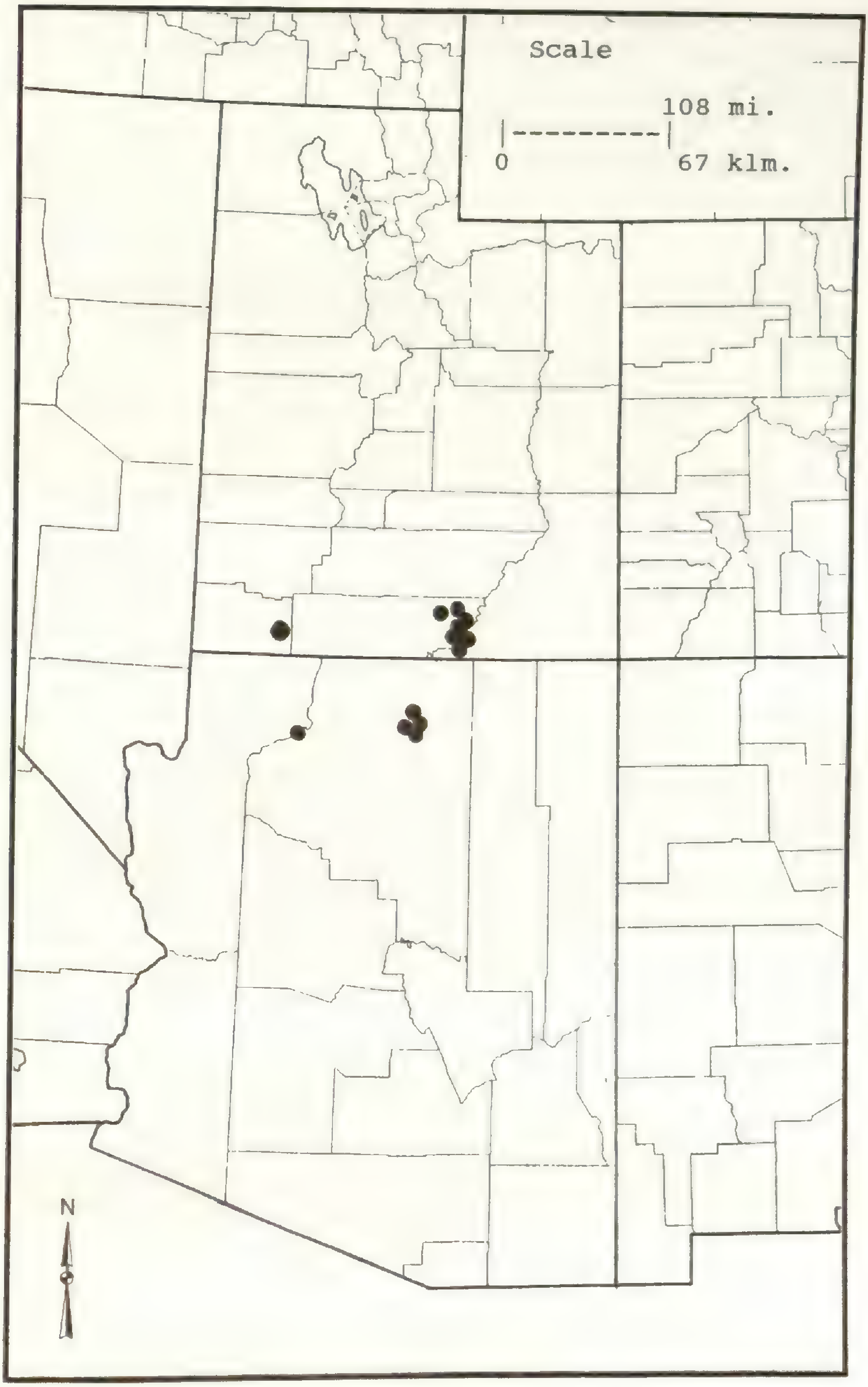
Scale
108 mi.
0
67 klm.
N

Figure 5. Distribution of *Carex curatorum*.

HABITAT. This taxon grows in riparian or hanging garden communities, and may have been represented by more populations before the damming and flooding of the Colorado River. It occurs on Navajo Sandstone, described as a crossbed of fine-grained sandstone and gray limestone (Lohman 1975), and on the Kayenta Formation, both of which are widespread substrata in southern Utah.

*Carex curatorum* is a distinct southwestern endemic. It is distinguished by sparsely pilose adaxial leaf surfaces, most obvious with the scanning electron microscope but visible with a dissection microscope. Achenes are not tightly enveloped by the perigynia and the pistillate scales are mostly shorter than the perigynia. The scales and perigynia are characteristically lighter in color than other taxa of section *Scirpinae.*

Plants flower from April to May. Upon maturity, the perigynia and enclosed achenes disarticulate from the spikes, and are readily dispersed, unlike *Carex scirpoidea* which retains achenes and perigynia sometimes until the next growing season. Maximum culm height is greater than that of *C. scirpoidea,* and the achene fills only a small portion of the perigynium. The unique achene micromorphology of *C. curatorum* and its sparsely pilose adaxial leaf surfaces segregate it from all other members of section *Scirpinae.*

In naming this species Stacey (1937) selected the epithet "curatorum" to honor Alice Eastwood and J. T. Howell, curators at the California Academy of Sciences, and the collectors of the type specimens. Stacey (1937) designated both a staminate and pistillate plant, on separate sheets and with different collection numbers, to serve as types. The pistillate specimen (*Eastwood & Howell 1100* CAS 204973), is selected herein to serve as the lectotype, since it possesses the diagnostic features of this taxon. The staminate specimen (*Eastwood & Howell 1101* CAS 204973) and two other specimens (*Eastwood & Howell 1045* CAS, *1089* CAS) collected along with the type remain important original material from the type locality.

*Carex haysii* Welsh, described in 1990, is treated here as a synonym since all the characters that are said to distinguish it overlap with *C. curatorum* except for perigynium length. However, on many specimens, the longest perigynia of *C. haysii* lacked fully formed achenes.

REPRESENTATIVE SPECIMENS: **United States.** ARIZONA: Coconino Co., Grand Canyon National Park, Kaibab Trail to Roaring Springs, 22 Sep 1938, *Eastwood & Howell 7073* (CAS, F, MICH, MT, NY, POM, UC, US, WTU); Grand Canyon National Park, False President Harding Rapids, mile 43, 17 Mar 1974, *Karpiscak & Theroux 941* (ARIZ); Colorado River, Buck Farm Canyon, 40.75 mi. below Lees Ferry, ½ mi. above river, 29 Apr 1970, *Holmgren, Holmgren & Ross 15481* (COLO); Mohave Co., Grand Canyon National Monument, Toroweap Pt., Saddle Horse Springs, 13 Jun 1941, *Cottam 8652* (COLO, UT); UTAH: Kane Co., confluence of San Juan & Colorado Rivers, on San Juan, ca. ⅛ mi. above second hanging garden on W in side-canyon, 9 Jun 1972, *Atwood 4094* (BRY); Glen Canyon National Recreation Area, Lake Powell, vicinity North Escalante, ca. 3800 ft., T40S R9E S36, 28 May 1983, *Welsh 22113* (BRY, NY); Long Canyon, Waterpocket Fold, T39S R9E S1, 24 May 1984, *Welsh 22850* (BRY); Coyote Creek Canyon, near Jacob Hamblin Arch, T38S R8E, 29 Jul 1985, *Dunlop & Orlando 2087* (NHA); Glen Canyon Nat. Rec. Area, Cow Canyon, Waterpocket Fold, T38S R9E S36, 26 Jul 1983, *Welsh, Welsh & Chatterley 22350* (BRY); San Juan Co., Lake Powell, Double Cove Garden, T40S R9E S25, 3800 ft., 1 Jul 1983, *Welsh 22322* (BYU, UT); Lake Powell, Ribbon Canyon, canyon sides and hanging gardens, T41S R10E S5, 25 Apr 1983, *Welsh 21730* (BRY); Washington Co., Zion Canyon, Lower Emerald Pool, Springdale Sandstone, hanging garden, sandy bank and cliff face, ca. 4300 ft., T41S R10W S9, 5 Jun 1989, *Welsh, Clark & Hays 24335* (BRY, CAS, NY, POM, RM UT); Kayenta Formation, ca. 6000 ft., Kolob Section, hanging garden below Kolob Arch, ca. 5 mi. SE of Kolob Canyon visitor center, T39S R12W S1, 25 May 1989, *Higgins 18499* (BRY, CAS, NY, RM, UT, UTC); Zion Canyon, Weeping Rock, T41S R10W S2, ca. 4300 ft., 9 Jul 1988, *Welsh, Clark & Charlesworth 24059b* (BRY); Zion Canyon, Lower Emerald Pool, Springdale Sandstone, hanging garden, ca. 4300 ft., T41S R10W S9, 2 May 1989, *Welsh & Clark 24233* (BRY).

## EXCLUDED TAXA

*Carex gigas* (Holm) Mackenzie, Bull. Torrey Bot. Club 35: 268. 1908. *Carex scirpoidea* var. *gigas* Holm, Amer. J. Sci. IV 18: 20. 1904. TYPE: U.S.A. California: Siskiyou County, Mt. Eddy (not known).

*Carex scabriuscula* Mackenzie, Bull. Torrey Bot. Club 35: 268. 1908. TYPE: U.S.A. Wet meadow in the Cascade Mountains, 30 Jun 1902, *Cusick 2849* (HOLOTYPE: NY!; ISOTYPES: CU!, DS!, ORE!, OSC!, POM!, UC!, WS!).

The taxonomic status of *Carex gigas* and *C. scabriuscula,* serpentine endemics in California and Oregon, remains problematic. These two taxa are excluded from section *Scirpinae* because they are rarely unispicate, often not dioecious, and do not possess the pubescence of the perigynia characteristic of the section. Exclusion is further supported by evidence from chromosome numbers, leaf surface features, and ecology (Dunlop 1990).

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## NEW ENGLAND NOTE

# RARE AND NON-NATIVE PLANTS OF MASSACHUSETTS' FLOODPLAIN FORESTS

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Six rare plant species occur primarily in floodplain forest communities in Massachusetts: *Arisaema dracontium, Betula nigra, Carex grayi, C. typhina, Mimulus alatus,* and *Rumex verticillatus.* Two of the species, *M. alatus* and *B. nigra,* are identified as regionally rare taxa (Division 2) on the *Flora Conservanda:* New England list (Brumback and Mehrhoff, et al. 1996), and all except *B. nigra* are protected species under the Massachusetts Endangered Species Act (Massachusetts Division of Fisheries and Wildlife 1997). In a statewide inventory and vegetation classification of Massachusetts' floodplain forest communities (Kearsley 1999), all six rare plant species were found to occur primarily in two of six identified community types: Transitional floodplain forests—*Acer saccharinum–Arisaema dracontium* association (Type III) and Small-river floodplain forests—*A. saccharinum–Fraxinus pennsylvanica–Quercus palustris* association (Type IV). Floodplain forest communities of Types III and IV appear to be less severely scoured and more poorly drained than Major-river types (Types I and II), but more well-drained than seasonally flooded *A. rubrum* Alluvial swamp forests (Type V).

In the Massachusetts floodplain forest inventory, *Arisaema dracontium* occurred primarily in floodplain forests classified as Type III. All current floodplain forest localities of *A. dracontium* are limited to the Connecticut, Deerfield, and Housatonic Rivers. Eleven of the thirty sites examined in the inventory and classification project that occur on the Connecticut, Deerfield, or Housatonic Rivers had vegetation classified as Type III, and *A. dracontium* occurred at six of those sites. All plots classified as Type III in the TWINSPAN analysis were clustered together with and without *A. dracontium* included in the analysis.

*Arisaema dracontium* did not occur at the nineteen sites on the Connecticut, Deerfield, and Housatonic Rivers with vegetation not classified as Type III, with the exception of one site on the Mill River in Northampton classified as a Small-river floodplain forest (Type IV). In addition to the six *A. dracontium* localities surveyed in 1997, six other current localities of *A. dracontium* are tracked in the Massachusetts Natural Heritage and Endangered Species Program (MNHESP) Biological and Conservation Database. These six sites were not included in the floodplain forest inventory because they are small and/or disturbed floodplain forest patches, but the associated species (*Acer saccharinum, Fraxinus pennsylvanica,* and *Ulmus americana* over a mixed herbaceous understory of *Boehmeria cylindrica, Laportea canadensis, Pilea pumila, Onoclea sensibilis,* and *Matteuccia struthiopteris*) closely match the species association of Type III floodplain forest communities.

The results of the floodplain forest inventory support Sanders' (1989) earlier findings that *Arisaema dracontium* populations occurred on Limerick and Hadley silt loams, but not on adjacent Winooski silt loams or Suncook loamy, fine sands along the Connecticut River. They also suggest that efforts aimed at locating and protecting *A. dracontium* populations should focus on Transitional floodplain forest communities (Type III).

*Carex grayi, C. typhina, Mimulus alatus,* and *Rumex verticillatus* were all found to occur primarily in floodplain forest sites classified as Type IV, which are characterized by a mixture of *Acer saccharinum, Fraxinus pennsylvanica,* and *Quercus palustris* over an open understory dominated by *Onoclea sensibilis* and *Boehmeria cylindrica* (Kearsley 1999). Sorrie (1987) previously described *C. grayi* as occurring in *F. pennsylvanica–A. saccharinum–Q. palustris–Populus deltoides* floodplain forests of the Connecticut and Housatonic Rivers. Of the twelve sites with vegetation classified as Small-river floodplain forests (Type IV; Kearsley 1999), four are current localities of *C. typhina,* two of the four sites are also localities for *C. grayi* and *M. alatus,* and one of the four provides habitat for all four rare plant species. Floodplain forest sites with vegetation not classified as Type IV generally did not contain these four rare plant species, with the following exceptions: two Transitional floodplain forest communities (Type III) on the lower Sawmill River in Montague and on the lower Housatonic River in Sheffield, which are current localities for *C. typhina* and *C. grayi,* respectively, one Alluvial terrace forest—*A. rubrum–Carya ovata–Prunus serotina* association (Type VI) on the Nashua River, which is a current locality for *C. typhina,* and the wet borders of a floodplain forest mosaic classified as both Types II and III on the Connecticut River in Longmeadow, Massachusetts, which is a current locality of *R. verticillatus.*

Current rare plant records compiled by MNHESP indicate that *Carex grayi, C. typhina, Mimulus alatus,* and *Rumex verticillatus* also occur in other floodplain communities not included in the recent inventory. These data provide further information about the habitat preferences of these species. *Carex grayi* occurs at five sites not included in the floodplain forest inventory—three sites are small patches of floodplain forest with vegetation associations that are most similar to Types III and IV, and two sites (on the Connecticut and Housatonic Rivers) have vegetation associations most similar to Alluvial terrace forests (Type VI), indicating that *C. grayi* may be found in all three floodplain forest habitats (Types III, IV, and VI). *Carex typhina* is found at one disturbed floodplain forest site not included in the inventory, but with vegetation most similar to Types III and IV. All current localities of *C. typhina* appear to be limited to Types III, IV, and V with most occurring in Type IV forests (five of nine current localities).

*Mimulus alatus* is known from two localities not included in the floodplain forest inventory, both are at the edges of small tributary creeks along the Connecticut River. The vegetation at these sites is most similar to that of Type IV Small-river floodplain forests, and *M. alatus* appears to be limited to low-energy stream bottoms of the Connecticut River Valley. *Rumex verticillatus* was found at two floodplain forest sites included in the current inventory: one at the border of a meander scar pool in a Small-river floodplain forest (Type IV) and one in the open, seasonally flooded borders of a large floodplain forest mosaic classified both as Major-river floodplain forest (Type II) and as Transitional floodplain forest (Type III) in depressions. *Rumex verticillatus* is known from two other localities in the state, a vernal pool complex and an emergent marsh, indicating that *R. verticillatus* is not strictly associated with a particular floodplain forest community, but rather with seasonally or semi-permanently inundated wetlands that can be associated with floodplain forests.

*Betula nigra,* which is a primarily southern tree, has a disjunct population in the Merrimack River Valley of southeastern New

Hampshire and northeastern Massachusetts (Burns and Honkala 1990). In Massachusetts, *B. nigra* is limited to sites on the Concord, Shawsheen, and Merrimack Rivers where it occurs as a riverbank tree in a narrow band along the Merrimack River, as an occasional associate within Alluvial swamp forests (Type V) or as the dominant tree in Small-river floodplain forests (Type IV; Kearsley 1999). In areas along the Shawsheen River in Essex County that appear to have been cleared, *B. nigra* occurred in dense thickets (10–30 cm diameter at breast height) over a subcanopy of *Acer saccharinum* saplings, suggesting that *B. nigra* may be replaced by *A. saccharinum.*

Of the 214 species identified in floodplain forest communities during the 1997 inventory (Kearsley 1999), 36, or 17%, were non-native. The most frequently encountered non-native plant species across all types were *Rhamnus frangula, Rosa multiflora, Celastrus orbiculata, Alliaria petiolata, Glechoma hederacea, Lysimachia nummularia, Lythrum salicaria, Myosotis scorpioides,* and *Polygonum cuspidatum.* There were clear distributional patterns of non-native plant species across Massachusetts' floodplain forest communities. *Alliaria petiolata, G. hederacea,* and *P. cuspidatum* were more prevalent on coarse-textured alluvial soils of Major-river floodplain forests (Types I and II). *Polygonum cuspidatum* was most often found on open, heavily-scoured banks, but it also occurred in dense monocultures in open areas within the interior forest. Preventing further canopy openings may be the only effective way to prevent the spread of *P. cuspidatum* in Major-river floodplain forests (Beerling et al. 1994). *Alliaria petiolata* and *G. hederacea* were found mainly along trails and did not appear to be spreading where the natural understory vegetation was intact. These two species were also the two most common exotic plant species in a study of the Potomac River floodplain forests in Virginia and Maryland (Pyle 1995).

*Rhamnus frangula, Celastrus orbiculata, Lysimachia nummularia, Myosotis scorpioides,* and *Lythrum salicaria* were more common on poorly-drained silt loams in the eastern part of Massachusetts (Types IV, V, and VI; Kearsley 1999). *Lysimachia nummularia, M. scorpioides,* and *R. frangula* covered broad areas at some sites. In two permanent plots monitored by the Massachusetts Audubon Society along the Ipswich River, the cover of *L. nummularia, R. frangula, L. salicaria,* and *M. scorpioides* increased by 50% and 83%, respectively over a six year period

(Anderson 1993). More studies are needed to monitor the spread of these taxa.

Although *Lythrum salicaria* is one of the most invasive wetland plants in the Northeast (Stein and Flack 1996), *L. salicaria* is largely absent from floodplain forest communities in Massachusetts. It occurred only along the wettest riverbanks in eastern Massachusetts and on sandy beaches on the Connecticut River. *Catalpa speciosa* has been reported to be increasing in abundance in at least one Connecticut River floodplain forest (Burk and Prabhu 1988), and we observed the trees in low but consistent numbers in floodplain forests of Types II, III, and IV (Kearsley 1999).

ACKNOWLEDGMENTS. I thank Paul Somers for his critical review of this note. Information on Massachusetts occurrences of state-protected rare species was obtained from the Massachusetts Natural Heritage and Endangered Species Program (MNHESP) Biological and Conservation Database. Multiple people assisted with the floodplain forest community inventory as acknowledged in Kearsley (1999). In particular, I would like to thank Pat Swain, Rebecca Anderson, Henry Woolsey, and the MNHESP staff. The floodplain forest inventory and classification work was in part funded by a State Wetlands Protection Development Grant from the U.S. Environmental Protection Agency.

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## BOOK REVIEW

*Wild Orchids Across North America: A Botanical Travelogue* by Philip E. Keenan. 1998. 340 pp. illus. ISBN 0-88192-452-0 $39.95 (hardback). Timber Press Inc., Portland, OR.

*Wild Orchids Across North America* is an intensely personal account of author Philip Keenan's love for our native orchids. His color photography has portrayed the alluring qualities of these plants so well it seems only the fragrance is missing. Many of the close-ups reveal not only the details of form and color, but have captured that crystalline quality of the floral tissue that adds an indefineable measure of beauty to the flowers of these exquisite plants. In this book, the author reminds us why we love plants. Orchids and orchid photography are food for the soul.

In an age of increasingly technical botanical books, the author has chosen instead to recount the main field trips he has taken in the past thirty years, often with friends and colleagues, in order to make his personal acquaintance with the orchids on this continent. In the thirty-eight short chapters we come to a fuller appreciation of the natural variation, ecology, and geographic distribution of North American Orchidaceae, but this is not, by any means, the whole story. Through orchids we come to understand much about the author himself. He is romantic. In chapter nine he describes the day he finds *Corallorhiza striata* near the base of a beautiful moss-covered limestone ledge on Flowerpot Island, off the Bruce Peninsula in the Great Lakes, and hastens to set up his tripod and camera. Then he "waits for a shaft of sunlight to penetrate a crack in the canopy, and transform, . . . what a moment before was an inconspicuous, nay, even dull, flower, into a peppermint-candy-striped beauty of shimmering garnets and rubies." When the light is just right, he takes the picture and then sits for an hour, "savoring the moment and writing in my journal." In chapter 33 he recounts an encounter with *Cypripedium californicum*: "From the first moment on the scene, I know this is something special, so special that my stomach begins to ache from the excitement . . . ." In writing this book, Philip Keenan relives those special moments where intellect and emotion intersect in the pursuit and appreciation of things wild. It is a story told in the first person by someone who is truly moved by the natural beauty of the living world around us. This is a book that kindred spirits will savor.

The author has included more than 170 color photos to illustrate 82 of the 145 species of orchids native to North America excluding Mexico and Florida. Twenty-three of the thirty-five native genera are illustrated including 11 of the 14 species of *Cypripedium,* 7 of the 8 species of *Listera,* and 17 of the 30 species of *Platanthera.* For many species, such as *Arethusa bulbosa, Calopogon tuberosus, Galearis spectabilis, Cypripedium reginae,* and *Triphora trianthophora,* there are photographs of the rare color forms often sought by orchid enthusiasts. These images are especially welcome as this type of information is not well preserved in traditional herbarium specimens.

This book will not only set a new standard for orchid photography, but it will serve as an excellent companion to the technical manuals that amateurs and professionals must ultimately use to identify members of the taxonomically difficult species groups such as the orange fringed- and the purple fringed-orchids in the genus *Platanthera,* the yellow lady's-slippers or *Cypripedium parviflorum* complex, and the ladies'-tresses belonging to the *Spiranthes cernua* complex. The photographs and discussions of these hybrid complexes will provide many useful benchmarks to those beginning to explore the diversity in these species groups.

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# NEBC MEETING NEWS

**January 1999.** "Proactive Wetland Restoration in Massachusetts" was presented by Charles Katuska of the Massachusetts state government's Executive Office of Environmental Affairs (EOEA). The objective of his talk was to discuss wetland restoration aspects of the state's Wetlands Restoration and Banking Program (WRBP), which began in March, 1994, as an effort to implement the state's policy of "no net loss of wetlands in the short-term and a net gain in the long-term." Katuska explained that wetlands constitute 12% of the state's land area or about 600,000 acres. Of these acres, about 20% represent salt water wetlands, including 45,000 acres of tidal flats. Massachusetts wetlands were once more abundant. He said about 28% of the state's wetlands at the time of colonization have been lost due to filling, draining, and other human activities. He started by explaining the program's definition of wetland restoration: "The act, process or result of returning a wetland or a former wetland to a close approximation of its condition prior to the disturbance." Thus, the restoration result would not be necessarily a totally pristine wetland; the area could possess invasive species and still be considered restored. He recognized two types of restoration, the first being "the reestablishment of a wetland or former wetland on what is now a nonwetland site," and the second being "the return of a damaged, degraded, or functionally impaired wetland to its predisturbance condition." Examples of restoration actions include restoring tidal flow, removing fill or dikes, regrading, planting wetland vegetation, and controlling invasive species. *Phragmites* control, thus far, has been a major activity of the WRBP. They have been working with coastal communities, in particular, where loss of the normal tidal influence has resulted in *Phragmites* overtaking *Spartina* in the tidal marshes, and they are now finalizing a *Phragmites* control strategy paper.

To accomplish their objectives, the two person staff of WRBP works with many other agencies, organizations, and individuals. To help cement such relationships, the state EOEA, along with a number of federal and state agencies, signed a joint resolution in June, 1994, committing to the restoration of Massachusetts wetlands. Along with the signatories, they have since formed an alliance with nearly 200 other agencies, organizations, and individuals who have agreed to work together toward implementing the

Commonwealth's "no net loss" Action Plan. A premise of the plan is that it is better to treat wetlands as part of a watershed than as isolated landscape features, thus "watershed wetland restoration plans" are being prepared, as well, with the assistance of members of the above "Partnership." Through WRBP, the U.S. Army Corps of Engineers has developed a site identification, data collection, and site screening analysis at the watershed scale. Using aerial imagery and other data, potential wetland restoration sites are identified and characterized, then the potential restoration projects are analyzed to determine their ability to positively influence wetland functions and the watershed as a whole. This technical analysis is based on simple functional predictors (size, position on the landscape, soil characteristics, hydroperiod, etc.) and assessment of "the watershed's functional deficits" in terms of water quality, flood storage, and fish and wildlife habitat. Individual site characteristics considered in the analysis also include factors such as ownership, cost, and likely difficulty of restoration efforts. The Neponset River watershed serves as the first test or pilot project for this watershed-based planning approach. In this watershed alone, 159 potential restoration sites were initially identified by the Corps in the preliminary assessment and six general goals for wetland restoration were established, including control of invasive species. Interestingly, when a draft plan for Neponset was reviewed by the citizenry, they identified "stream baseflow and groundwater recharge" as an additional watershed goal, as well as identifying 12 additional potential wetland restoration sites. Plans for six other watersheds (Otter River, Paskamanset River, Upper Ipswich, Shawsheen, Upper Blackstone, and Connecticut River) are in the works, as well as salt marsh inventories along the coast.

The intent of the WRBP is to have implementation of restoration projects locally driven. Thus they do alot to encourage proposals and funding of projects. One way is through the GROWetlands initiative whereby they seek and accept project nominations. The WRBP then helps with technical support, coordination, permitting, access to its read-only database of other wetland restoration projects, and funding. Katuska finished with an invitation to the NEBC to help, especially with invasive plant projects, and then offered handouts describing WRBP, GROWetlands, and 25 funding sources available for wetland restoration projects in the Commonwealth.

**February 1999.** The speaker for the evening was Dr. Janet Sullivan, Editor-in-Chief of *Rhodora* and adjunct faculty in botany at the University of New Hampshire, who addressed the topic, "Reflections on 100 years of *Rhodora.*" Janet's talk began with Volume 1, Number 1 of *Rhodora* dated January, 1899. The Editor-in-Chief was Benjamin Lincoln Robinson and Associate Editors were Frank Shipley Collins, Merritt Lyndon Fernald, and Hollis Webster. Subscribers each paid a dollar for a dozen issues the first year. The stated purpose of the journal was "to give new stimulus and render material aid to the study of our local flora." Unlike today, the editors announced in the first issue that contributors could follow their own preferences regarding nomenclature and punctuation. All four members of the editorial committee, especially M. L. Fernald, were frequent contributors the first year and for many to follow. The early issues contained mostly short articles and notes, reports and historical accounts of other botanical clubs such as the Josselyn and the Connecticut Botanical Clubs, upcoming events, and appeals for information on the region's flora.

The idea for the journal, Sullivan explained, arose shortly after the Club's first meeting in February, 1896. The described purpose of the Club and its meetings was to provide for social discourse and the dissemination of information among gentlemen interested in the flora of New England. A specific goal, to create a checklist of the New England flora, helped lead the way to establishment of the journal. In the fall of 1897, the Club reproduced Collins' list of algae using a hectograph process, which involved writing on a gel pad which was printed using aniline dye, somewhat like the later mimeograph process. Members of the Club then began investigating the possibility of a journal. In February, 1898, Robinson's Publication Committee reported that the cost of publishing a monthly journal of about 16 pages each issue would be about $550 per year, and recommended that the cost of plates be supported by "dignified ads," thus making them free to the authors and subscribers. E. L. Rand recommended a minimum of 400 subscriptions would be necessary to support the journal. A circular was distributed to members in April, 1898, requesting that resident members in the Boston area each solicit ten subscriptions and nonresidents each obtain five. This resulted in 450 subscriptions and the journal was launched in earnest. Debate ensued over the name for the new journal. Robinson stated that the name should be a "distinct and euphonious one-word title." Rand, in botanical jest, suggested the name *Taxus*; other suggestions were *Oakesia* and *Bigelovia.* The name *Rhodora* was suggested but considered "too sentimental" by some, presumably because of Emerson's poem by the same title. In the end, however, there were 15 votes for *Rhodora* and 11 votes for all other names suggested. The name was presented to the Club at the November, 1898, meeting. Subscriptions had increased to around 600 and the Club had launched its journal to reach "the botanical world, who knows us not."

Once the journal was established, Collins' paper on algae and others, such as one by Walter Deane, presenting New England's state by state distribution of taxa in the Ericaceae, began to appear. Costs, however, were higher than originally estimated, due mainly to indexing and electrographic printing costs, and the Club ran a deficit for several years. More ads were included to defray the cost of plates, an item deemed essential to attract and hold subscribers. Ads in the early volumes represented nurseries, booksellers, personal herbaria, and field guides. Following the Club's July, 1900, "excursion" to Mt. Katahdin in Maine and an account of it in Volume 3 by Joseph R. Churchill, an ad appeared offering "To Katahdin on horseback." Other ads offered to guide readers to rare plant locations. Controversy over the latter led to ads being dropped in 1907. In 1912, subscription prices were raised to $1.50 per year. An obstacle to printing Volume 2 arose when a fire destroyed the press where it was to be printed. At the time, however, the page proofs were being circulated to authors and the plates were being stored in a vault, so only a three-week delay occurred.

In the early volumes the editors were also major contributors as authors. In the first volume, for instance, they contributed 28% of the articles. M. L. Fernald alone contributed 15 articles. Even today, he ranks as the most prolific writer in the pages of the journal. In one year he wrote 25 articles and notes, and over a 52-year span from 1899 to 1950 he averaged 13 contributions per year. His role as Associate Editor continued until 1928 when he became Editor-in-Chief, a position he held until 1950. "Could it have survived without his energy?" some have asked. Gradually, though, the authorship did diversify. In his thirty-year review article published in 1929, Fernald noted that 399 botanists had contributed to the pages of *Rhodora* thus far.

Reed Rollins succeeded Fernald as Editor-in-Chief. In 1962, when Rollins eventually resigned, Albion Hodgdon from the University of New Hampshire became the first Editor-in-Chief from outside Boston, the journal became a quarterly publication with a subscription cost of $6.00. Another milestone occurred in 1996 when our speaker, Janet Sullivan, became the tenth, and first female Editor-in-Chief, particularly notable because women were not admitted to the Club until 1968. The journal itself continues to serve botanists of New England but has broadened its readership and geographic scope to an international level, something that actually began as early as 1919, when F. S. Collins published an article on marine algae of China.

—PAUL SOMERS, Recording Secretary.

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FLORAS AND TAXONOMIC TREATMENTS: Specimen citation should be selected critically, especially for common species of broad

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# RHODORA

## Journal of the New England Botanical Club

### CONTENTS

Notes on *Acalypha* (Euphorbiaceae) in North America. *Geoffrey A. Levin* .... 217

The freshwater species of *Vaucheria* (Tribophyceae, Chrysophyta) from Connecticut. *Craig W. Schneider, Christopher E. Lane,* and *Anna Norland* .... 234

Disturbance as a factor in the distribution of sugar maple and the invasion of Norway maple into a modified woodland. *Rebecca Anderson* .... 264

*Cardamine georgiana* (Brassicaceae), a new name replacing *Dentaria microphylla*. *Ihsan A. Al-Shehbaz* and *Suzanne I. Warwick* .... 274

Covariance of lichen and vascular plant floras. *James P. Bennett* and *Clifford M. Wetmore* .... 277

NEW ENGLAND NOTES

Notes on the habits and life-history of *Bidens discoidea*: An epiphyte in Massachusetts floodplain ponds. *Matthew G. Hickler* .... 298

A new Barnstable County, MA, record for *Asclepias purpurascens*. *Donald G. Schall, Mario J. DiGregorio,* and *Pamela Polloni* .... 300

*Cyperus microiria*: A new addition to the flora of Connecticut. *Tad M. Zebryk* .... 302

BOOK REVIEWS

Proceedings of a Symposium on the Recovery and Future of the Northeastern Forest, Connecticut College, April 12, 1997 .... 303

Discovering the Unknown Landscape: A History of America's Wetlands .... 306

Flora of Maine: A Manual for Identification of Native and Naturalized Vascular Plants of Maine .... 309

NEBC MEETING NEWS .... 311

ANNOUNCEMENTS

New England Botanical Club Graduate Student Research Award .... 318

Humboldt Field Research Institute Prize .... 319

Information for Contributors .... 320

NEBC Membership Form .... 322

NEBC Officers and Council Members .... inside back cover

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# The New England Botanical Club, Inc.

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# RHODORA

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# NOTES ON *ACALYPHA* (EUPHORBIACEAE) IN NORTH AMERICA

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ABSTRACT. Studies of three groups of North American *Acalypha* (Euphorbiaceae) species are presented. *Acalypha hederacea* and *A. monostachya* have traditionally been separated by plant sexuality and staminate inflorescence length, but examination of specimens from throughout the ranges of these two taxa show that they do not differ in either character. *Acalypha hederacea* should be treated as a synonym of *A. monostachya. Acalypha lindheimeri* and *A. phleoides* supposedly differ in toothing of the bracts subtending the pistillate flowers and in the shape of the leaf apices. However bract toothing is highly variable among these plants and leaf apex shape varies clinally, with numerous intermediates. *Acalypha lindheimeri*, based on specimens both geographically and morphologically extreme, should be treated as a synonym of *A. phleoides*. The *A. virginica* group has a complex taxonomic history. Taxonomic confusion has resulted from emphasis on characters that are unreliable because they show overlapping variation among the taxa. Five species can be distinguished based on unambiguous, nonoverlapping characters.

Key Words: *Acalypha, A. monostachya, A. phleoides, A. virginica*, Euphorbiaceae

In the course of my studies of *Acalypha* (Euphorbiaceae) for *Flora of North America* (Levin, in press), I have had to address several taxonomic problems in this large genus. Here I present the results of those investigations in more detail. There has not been a comprehensive study of the North American species of *Acalypha* published since Pax and Hoffman (1924) reviewed the entire genus. However, Miller (1964) studied the native species with varying depth and McVaugh (1961) studied two of the species that have distributions extending south into Mexico. In addition, the *A. virginica* group has received considerable attention (Cooperrider 1984; Reveal et al. 1990; Weatherby 1927, 1937, 1940).

## *ACALYPHA MONOSTACHYA* CAV. AND *A. HEDERACEA* TORR.

*Acalypha hederacea* and *A. monostachya* have generally been distinguished by the length of the staminate spikes (Müller 1866;

Pax and Hoffmann 1924), with those of *A. hederacea* said to be about 6 cm long vs. 2–3 cm in *A. monostachya*. Plants assigned to both species are widespread in Mexico, but those in the United States have generally been called *A. hederacea*. McVaugh (1961) argued that the spikes of specimens generally called *A. hederacea* were rarely longer than 3 cm and often less than 2 cm, and therefore proposed that the taxa were not distinct. In contrast, Miller (1964) stated that the staminate spikes of *A. hederacea* averaged about 3.5 cm based on both measurements across the geographic range of the species and a population sample (presumably from Texas). Elsewhere Miller (1970) gave the length as 16–84 mm. She nowhere gave lengths for *A. monostachya*. Miller (1964) also argued that *A. hederacea* is mostly dioecious and generally has both terminal and axillary pistillate spikes, and implied that *A. monostachya* is monoecious and has strictly axillary pistillate spikes (both species, according to Miller and all other authors, have exclusively terminal staminate spikes). In the only other source of original observations, Johnston and Warnock (1962) studied *A. hederacea*. They gave the length of the staminate "thyrses"—presumably meaning the fertile portion of the inflorescence because they said the thyrses are peduncled—as "1–3 (–6) cm" and stated that the plants were usually monoecious. None of these authors studied type material of *A. monostachya*, although both McVaugh (1961) and Miller (1964) discussed Cavanilles' (1800) illustration of this species. Miller (1964) apparently examined four of the seven syntypes of *A. hederacea*, but there is no indication McVaugh (1961) or Johnston and Warnock (1962) studied any of the type material.

**Sexuality**. I studied about 250 specimens from throughout the range of this complex from GH, LL, MICH, MO, NY, and TEX (herbarium abbreviations follow Holmgren et al. 1990). I observed three types of plants: pistillate flowers only, staminate flowers only, and monoecious (those with both staminate and pistillate flowers). Pistillate plants bore both axillary and terminal spikes, whereas staminate plants bore strictly terminal, long-pedunculate spikes. Inflorescence distribution on the monoecious plants was more complicated. Staminate flowers were always produced in terminal spikes. These were sometimes unisexual, but more often androgynous with one to three pistillate flowers near the base of the peduncle. On most monoecious plants the pistillate spikes were all axillary, but some monoecious plants also bore terminal pistillate spikes.

I was able to locate five of the seven syntypes of *Acalypha hederacea*. Four of these (*Bigelow s.n.*, *Edwards & Eaton s.n.*, *Wright 648*, *1814*) consist of unisexual plants, whereas *Wright 1813*, from Texas, is monoecious, with axillary pistillate spikes and terminal androgynous spikes bearing a single pistillate flower near the base of the peduncle of the otherwise staminate spikes. The type of *A. monostachya* was not designated, but apparently is *Née s.n.* (MA), the specimen itself from a plant cultivated at Madrid (R. McVaugh, pers. comm.). I haven't seen this specimen, but presumably it was the model for Cavanilles' (1800) illustration, which shows a monoecious plant with axillary pistillate inflorescences.

It is difficult to assess the sexuality of populations from herbarium specimens, because most collections consist of just a single plant. However it is still clear that within the *Acalypha hederacea/monostachya* complex, sexuality varies geographically. In the northern part of the range, both unisexual and monoecious plants are common, and from collections it appears that populations may consist of unisexual plants or may be mixed monoecious and pistillate. In only one case, *Marsh 3111* (TEX), from Coahuila, did I observe both staminate and monoecious plants in a single collection; this collection also included pistillate plants. Farther south, monoecious plants predominate and unisexual plants are almost absent. For example, of 55 specimens I observed from the Mexican states of Aguascalientes, Durango, Guanajuato, Hidalgo, Oaxaca, Puebla, Queretaro, San Luis Potosí, and Zacatecas, 51 were monoecious, two (one each from Guanajuato and Hidalgo) were pistillate, and two (one each from Durango and Hidalgo) were staminate.

To quantify this variation, I used the proportion of monoecious plants among all plants bearing staminate flowers, i.e., the sum of staminate plus monoecious plants. I used this statistic for two reasons. First, pistillate plants are likely to be over-represented in collections because the pistillate spikes persist longer than the staminate spikes. Second, as I discussed before, populations with monoecious plants may also contain pistillate plants, especially in the northern part of the range of the complex. Measured this way, Texas had the lowest frequency of monoecious plants, 56%. The northern tier of Mexican states (Chihuahua, Coahuila, Durango, Nuevo León, and Tamaulipas) had a higher rate of 80%, and the remaining eight Mexican states within the range had an overall rate of 98%, with many having no staminate plants at all. Although the frequency of monoecious plants clearly increases southwards ($\chi^2$ test using the three geographic areas, $P < 0.0001$), monoecious plants are common throughout the range of the complex.

As might be expected because of the geographic pattern in sexuality and the historical identification of northern plants as *Acalypha hederacea* and southern plants as *A. monostachya*, there is a strong association between determination and sexuality ($\chi^2$ test, $P < 0.0001$). About 68% of sampled plants historically determined as *A. hederacea* were monoecious, whereas 96% of *A. monostachya* were monoecious. Clearly, though, monoecy is common, even among plants that have been called *A. hederacea*. This result is consistent with McVaugh (1961) and Johnston and Warnock (1962), but not with Miller (1964, 1970).

**Staminate spike length**. I measured the staminate or androgynous spike length on the 191 specimens containing mature staminate or monoecious plants. Of these, 50 were determined as *Acalypha hederacea* and 141 as *A. monostachya*. The staminate and androgynous spikes consist of two portions, the peduncle and the fertile staminate portion, which I measured separately. To explore geographic variation, I divided the range into three regions, Texas, northern Mexico (Chihuahua, Coahuila, Durango, Nuevo León, and Tamaulipas), and central/southern Mexico (Aguascalientes, Guanajuato, Hidalgo, Oaxaca, Puebla, San Luis Potosí, and Zacatecas), and randomly sampled 48 specimens from each (48 was chosen because that was the number of specimens available from the third region). Peduncle length, staminate portion length, and total spike length did not significantly differ among the three areas (Table 1).

I also tested for differences between monoecious and staminate plants, and between plants historically determined as *A. hederacea* and *A. monostachya*, using all 191 specimens. Lengths of the peduncle, staminate portion, and total spike did not significantly differ by plant sexuality (Table 2A) or by historical determination (Table 2B). Among all the specimens, the length of the fertile portion of the staminate spike was 1–4 cm (mean = 2.1 cm) and the total length of the spike was 1.9–7.9 cm (mean = 4.0 cm).

Table 1. Regional variation in staminate and androgynous inflorescence dimensions that have been used to distinguish *Acalypha hederacea* and *A. monostachya*. Regions are A: Texas, B: northern Mexico (Chihuahua, Coahuila, Durango, Nuevo León, and Tamaulipas), and C: central and southern Mexico (Aguascalientes, Guanajuato, Hidalgo, Oaxaca, Puebla, Queretaro, San Luis Potosí, and Zacatecas). Lengths are shown as mean ± standard error based on 48 herbarium specimens from each region. Probabilities are for the given *F* values obtained by one-way analysis of variance.

| | Region | | | | |
|---|---|---|---|---|---|
| | A | B | C | *F* | *P* |
| Peduncle length (cm) | 1.84 ± 0.073 | 1.98 ± 0.084 | 2.03 ± 0.103 | 1.305 | 0.274 |
| Staminate portion length (cm) | 2.08 ± 0.083 | 2.10 ± 0.084 | 2.22 ± 0.096 | 0.745 | 0.477 |
| Total inflorescence length (cm) | 3.92 ± 0.140 | 4.04 ± 0.153 | 4.25 ± 0.177 | 1.134 | 0.325 |

Table 2. Comparison of staminate and androgynous inflorescence dimensions that have been used to distinguish *Acalypha hederacea* and *A. monostachya.* Herbarium specimens are classified according to (A) sexuality (unisexual plants vs. monoecious) and (B) original determination (*A. hederacea* vs. *A. monostachya*). Lengths are shown as mean ± standard error. Probabilities are based on two-tailed *t*-tests assuming unequal sample variances.

A. Plant Sexuality

| | Unisexual Plants (n = 47) | Monoecious (n = 144) | *t* | *P* |
|---|---|---|---|---|
| Peduncle length (cm) | 1.85 ± 0.065 | 1.95 ± 0.051 | 1.176 | 0.242 |
| Staminate portion length (cm) | 2.06 ± 0.085 | 2.14 ± 0.053 | 0.845 | 0.400 |
| Total inflorescence length (cm) | 3.91 ± 0.133 | 4.10 ± 0.093 | 1.122 | 0.265 |

B. Original Determination

| | *A. hederacea* (n = 141) | *A. monostachya* (n = 50) | *t* | *P* |
|---|---|---|---|---|
| Peduncle length (cm) | 1.89 ± 0.046 | 2.04 ± 0.092 | 1.522 | 0.132 |
| Staminate portion length (cm) | 2.12 ± 0.052 | 2.14 ± 0.093 | 0.235 | 0.815 |
| Total inflorescence length (cm) | 4.00 ± 0.088 | 4.18 ± 0.163 | 0.979 | 0.330 |

These results do not support the use of staminate spike length to distinguish *Acalypha hederacea* and *A. monostachya.* It is possible that the complex has two species, differing in sexuality, with broadly overlapping geographic ranges. However, I found no other morphological features that differentiate two groups. I suspect that Miller (1964) studied relatively few specimens (she gave no sample size) and that she measured the entire staminate spike, whereas McVaugh (1961) measured only the fertile staminate portion, hence the differences in their observations. When interpreted this way, their measurements are consistent with mine. Because I can find no way to distinguish two species, I agree with McVaugh (1961) that only a single species is involved, which should be called *A. monostachya.*

## *ACALYPHA PHLEOIDES* CAV. AND *A. LINDHEIMERI* MÜLL. ARG.

*Acalypha phleoides* is traditionally interpreted as a species of the arid highlands of eastern and central Mexico, ranging as far north as Chihuahua and Coahuila. Overlapping with this in northern Mexico and extending into Arizona, New Mexico, and Texas, is what is usually called *A. lindheimeri*. According to Müller (1866), *A. lindheimeri* has acuminate rather than acute leaves, the terminal tooth of the bracts subtending the pistillate flowers prolonged rather than equal to the other teeth, and more slender style branches.

I examined more than 400 specimens from throughout the range of these two taxa. Leaves on plants from Texas are mostly rhombic-ovate and acuminate, though lower leaves tend to be broader relative to their length and have acute apices. Sometimes the bracts subtending the pistillate flowers have elongate terminal teeth, as they do on two of the isosyntypes of *Acalypha lindheimeri* I have seen (*Lindheimer 520* [CAN!, GH!, MO!] and *Lindheimer 688* [GH!, MO!]), but more often all the teeth are subequal, as they are on the third isosyntype I examined (*Wright 1815* [GH!]). Leaves of plants from central Mexico south are ovate to suborbicular (especially the lower leaves) with consistently acute apices. The teeth of the bracts subtending the pistillate flowers are consistently subequal. There is also a tendency for the more southerly plants to have denser and coarser pubescence than the more northerly plants, especially those from Texas. Plants from Arizona, e.g., *Blumer 1498* (ARIZ!, GH!, ISC!, NMC!; the type of *A. lindheimeri* var. *major* Pax & K. Hoffm.), and northern Mexico are intermediate between the Texan and central Mexican plants, with no obvious discontinuities. I could distinguish no differences in style branch thickness. The difficulty of quantifying leaf shape and its variation within individual plants makes statistic analysis extremely problematic. However, because leaf shape varies apparently continuously throughout the range of the group and bract toothing shows no consistent pattern, it appears that *A. lindheimeri* was based on a few extreme specimens of *A. phleoides*. It therefore seems preferable to treat all these plants as a single species using the older name, *A. phleoides*.

## *ACALYPHA VIRGINICA* GROUP

The *Acalypha virginica* group has received the greatest study of any North American members of the genus. Through much of the 18th and 19th centuries, there was considerable disagreement in interpretation of this group, but most authors recognized either one or two taxa. Müller (1865, 1866), however, recognized four taxa in the group, all as varieties of *A. virginica*. In a series of papers, Weatherby (1927, 1937, 1940) attempted to sort out the variation in the group and to resolve a nagging typification problem surrounding the name *A. virginica*. Ultimately he recognized three species, *A. gracilens* A. Gray with three varieties [var. *gracilens*, var. *fraseri* (Müll. Arg.) Weath., and var. *monococca* Engelm. ex A. Gray], *A. rhomboidea* Raf. with two varieties [var. *rhomboidea* and the newly described var. *deamii* (Weath.) Weath.], and *A. virginica*. Unfortunately, the typification problem was not finally resolved until 1990 (Reveal et al. 1990), when conservation of the name and type of *A. virginica* established Weatherby's (1937) treatment.

Weatherby's treatment (1937) continues to be widely used today. However, two additional treatments have also had some influence. First, Miller (1964, 1969, 1970; Gandhi and Hatch 1988) recognized five species in the group, *Acalypha deamii* (Weath.) H. E. Ahles, *A. gracilens*, *A. monococca* (Engelm. ex A. Gray) Lill. W. Miller & Gandhi, *A. rhomboidea*, and *A. virginica*. In addition to segregating *A. monococca* as a separate species, she further realigned *A. gracilens* by treating var. *fraseri* as a synonym of *A. gracilens* var. *gracilens* and recognizing *A. gracilens* var. *delzii* Lill. W. Miller. The second treatment was by Cooperrider (1984, 1995). Studying almost exclusively plants from Ohio and therefore not considering *A. gracilens* or *A. monococca*, he treated the remaining three taxa as varieties of *A. virginica* [thus *A. virginica* var. *deamii* Weath., *A. virginica* var. *rhomboidea* (Raf.) Cooperr., and *A. virginica* var. *virginica*].

In justifying his treatment, Cooperrider (1984) stated that he saw many intermediates between his varieties of *Acalypha virginica*, particularly between var. *rhomboidea* and var. *virginica*, and further that "no single reliable diagnostic character or combination of characters" separates these taxa. Based on my observations, I disagree. Instead, the apparent intergradation and lack of diagnostic characters reflect two problems. First, most of the characters used by Weatherby (1927, 1937) and Miller (1964, 1970) are not always reliable. Second, and clearly related to the first, misidentifications are rife in herbaria. On the approximately 4,000 specimens of *A. rhomboidea* and *A. virginica* I examined, about 18% of the annotations applied since 1940 (sufficiently after Weatherby's publications to allow them to become widely used) were misidentified, about half of these bearing names of the other taxon. (In this calculation I excluded Miller's annotations, with which I almost entirely concur.) Cooperrider's own identifications are instructive. I have seen 96 specimens of the two species he annotated. We agree on almost all that he called *A. virginica* var. *rhomboidea*, but we would agree on only 44% (eight of 18) that he called *A. virginica* var. *virginica*. Perhaps this high frequency of misidentifications prevented him from seeing the clear and reliable distinctions between these taxa. I found a similar rate of misidentifications among specimens of *A. gracilens* and *A. virginica*. (Another consequence of the high rate of misidentifications is that most published range maps are not reliable.)

Most regional floras that treat several taxa in the *Acalypha virginica* group (e.g., Cooperrider 1995; Gleason and Cronquist 1991; Miller 1970; Mohlenbrock 1982, 1986; Radford et al. 1968; Steyermark 1963) distinguish them using some combination of stem pubescence (long spreading and short incurved vs. just short incurved), petiole length (either absolute or relative to leaf length), leaf shape, shape and number of teeth or lobes on the bracts subtending the pistillate flowers, pubescence on these bracts, carpel number, and seed size. Table 3 summarizes these characteristics for the five species recognized by Miller (1964, 1970) and me. Some of these characters are unambiguous and serve to distinguish individual taxa. For example, *A. virginica* is unique in having long spreading eglandular trichomes on the abaxial surface of the pistillate bracts, and mature plants always bear these (the lowermost bracts on the plant may lack the spreading hairs, however). Similarly, *A. deamii* always has gynoecia with two carpels and *A. monococca* has gynoecia with one carpel, whereas the remaining species have three carpels. Also *A. deamii* has seeds that are at least 2.2 mm long, whereas the other species have seeds no more than 2.0 mm long, with the exception of *A. monococca*, which occasionally has seeds to 2.4 mm long. Outgroup comparison with *A. alopecuroides* Jacq., *A. arvensis* Poepp., *A. australis* L., *A. brachystachya* Hornem., *A. indica* L., and *A. mexicana* Müll. Arg. suggests that these unique characteristics are all apomorphies of the individual species (Table 3).

Other characters may be useful in separating otherwise similar species. A sample of 100 specimens each of *Acalypha virginica* and *A. rhomboidea* showed that the number of lobes on the pis-

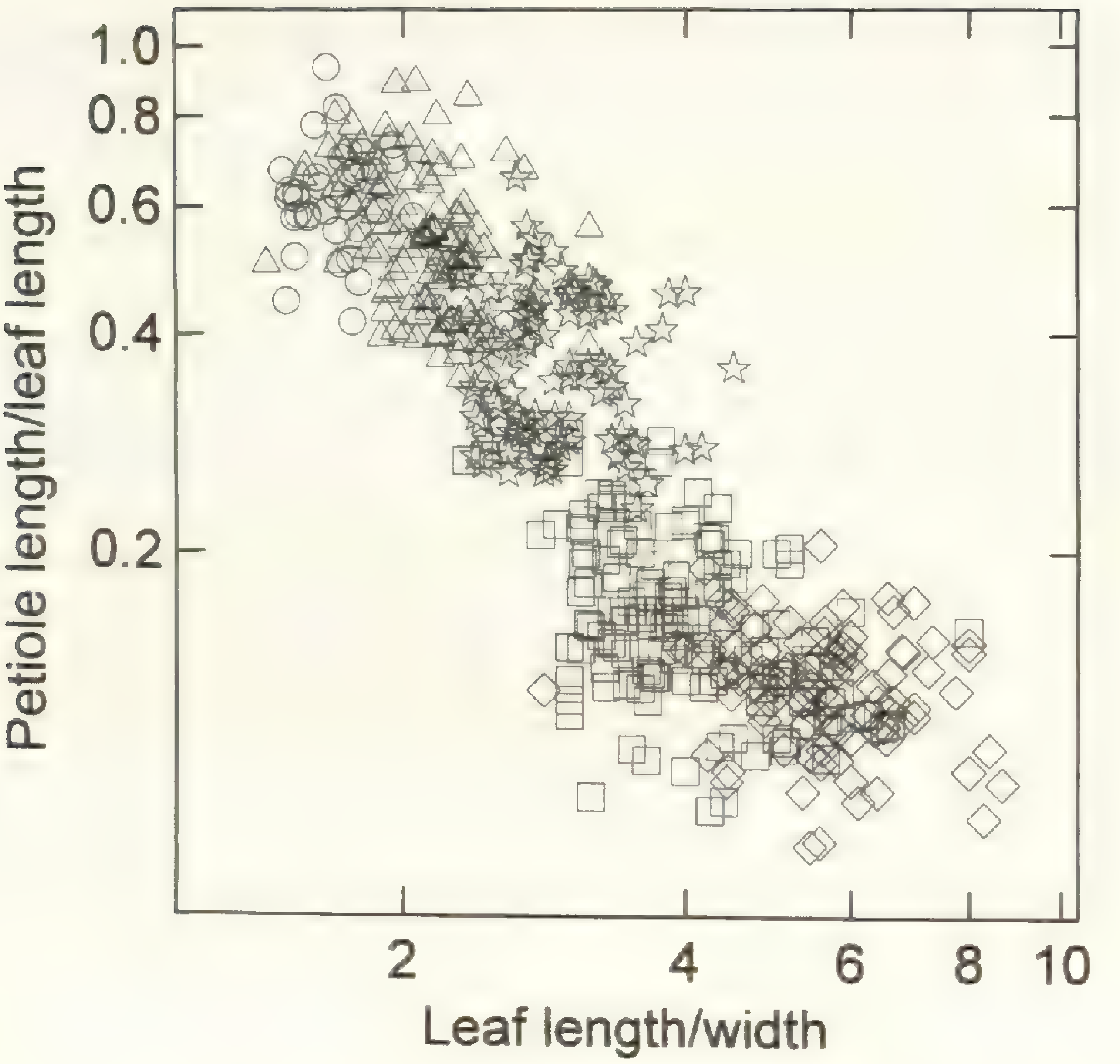
Table 3. Summary of characters often used to separate species in the *Acalypha virginica* group, compiled from herbarium specimens from throughout the geographic ranges of the species. Values for quantitative characters are ranges. Sample sizes are n = 100 except for *A. deamii*, a rare species for which n = 35. Asterisks (*) indicate unambiguous unique species-level apomorphies based on outgroup comparison with *A. alopecuroides*, *A. arvensis*, *A. australis*, *A. brachystachya*, *A. indica*, and *A. mexicana*.

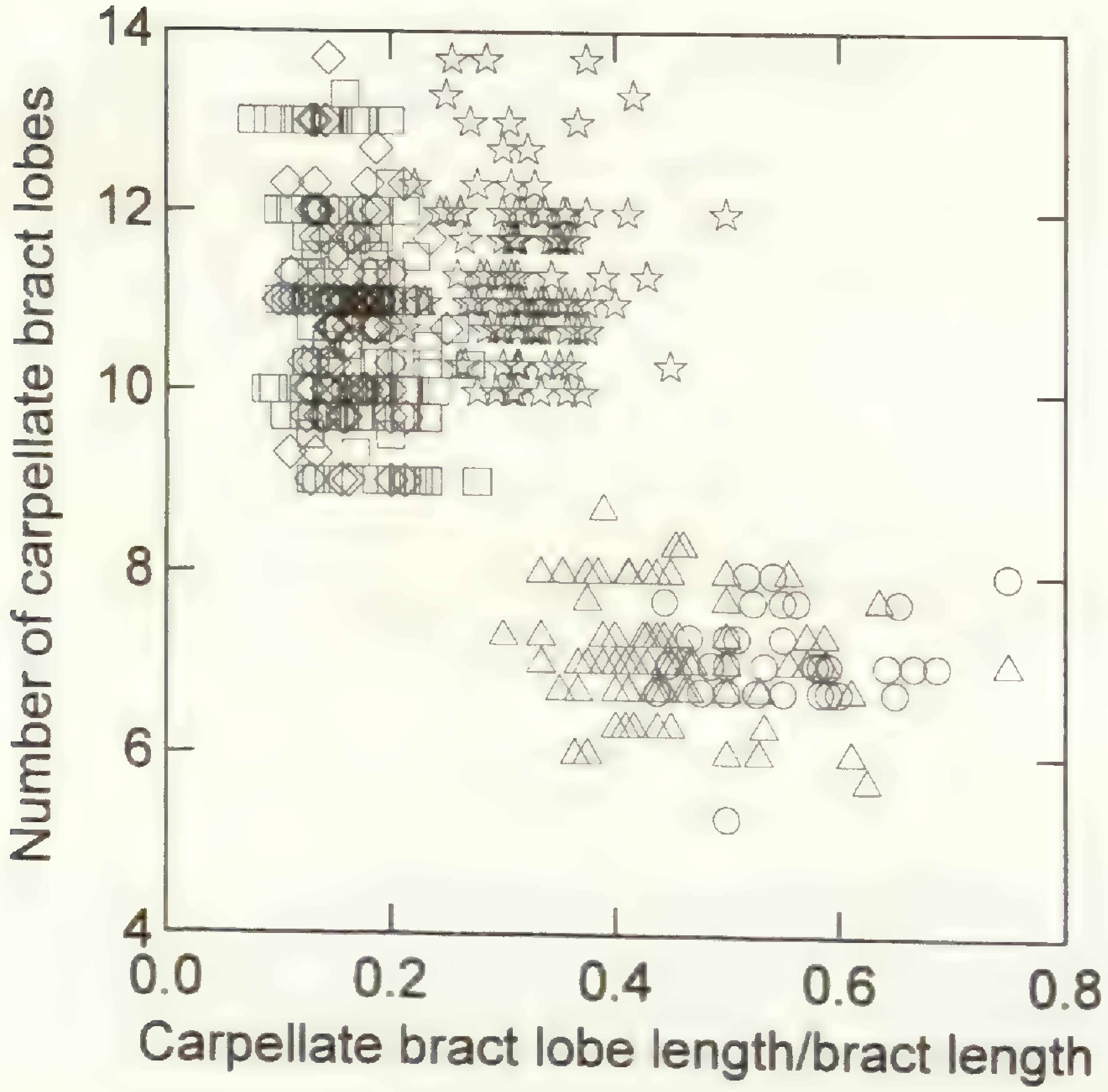
| Character | *A. deamii* | *A. gracilens* | *A. monococca* | *A. rhomboidea* | *A. virginica* |
|---|---|---|---|---|---|
| Stems with long spreading hairs | Never | Never | Never | About 5% of plants | About 90% of plants |
| Petiole length (cm) | 2.5–7.0 | 0.2–1.4 | 0.2–0.9 | 0.8–7.0 | 0.7–3.6 |
| Petiole length/leaf blade length | 0.42–0.94 | 0.09–0.30 | 0.08–0.20 | 0.34–0.89 | 0.23–0.66 |
| Leaf blade length/width | 1.5–2.0 | 2.3–8.0 | 2.8–8.7 | 1.4–3.2 | 2.1–4.5 |
| Pistillate bracts with long spreading eglandular hairs | No | No | No | No | Yes (except sometimes the lowermost on the plant)* |
| Pistillate bracts with red glands | No | Yes | Yes | No | No |
| Pistillate bract tooth (lobe) length (mm) | 4.5–9.0 | 0.6–2.2 | 0.9–2.2 | 1.8–9.0 | 1.6–5.0 |
| Pistillate bract tooth (lobe) length/pistillate bract length | 0.44–0.75 | 0.08–0.28 | 0.10–0.25 | 0.30–0.75 | 0.21–0.50 |
| Number of teeth/lobes on pistillate bracts (average of 3–5 bracts) | 5.3–8.0 | 9.0–13.3 | 9.0–13.7 | 5.7–8.7 | 10.0–13.7 |
| Carpel number | 2* | 3 | 1* | 3 | 3 |
| Seed length (mm) | 2.2–3.1* | 1.1–1.9 | 1.6–2.4 | 1.3–2.0 | 1.3–1.8 |

tillate bracts is a reliable character distinguishing these species. It is true that individual bracts of *A. rhomboidea* may have as many as nine lobes and bracts of *A. virginica* may have as few as nine lobes. However, averaging three to five bracts per plant gave no more than 8.7 lobes/bract for *A. rhomboidea* and no fewer than 10 lobes/bract for *A. virginica* (Table 3; Figure 1). The presence of red glands on the pistillate bracts, at least on the tooth apices and often scattered on the abaxial surface, distinguishes *A. gracilens* from very young plants of *A. virginica* that have not yet produced bracts with spreading trichomes. (*Acalypha monococca* also produces these red glands.) A particularly interesting situation that has not been noted previously is that scattered throughout the range of *A. rhomboidea*, but more frequent in the southern states, are small plants with short petioles, small leaves, and small pistillate bracts with short teeth. These often appear in herbaria labeled *A. gracilens*, presumably because of the short petioles and bract teeth. However, tooth number is consistently nine or fewer, the petioles are at least 40% the length of the leaf blades, the bract teeth are more than 30% the length of the bracts, and the bracts do not bear red glands. These characteristics clearly demonstrate that these plants are simply small *A. rhomboidea* rather than *A. gracilens* (Table 3; Figure 1).

Some characteristics that are frequently used to distinguish species in the *Acalypha virginica* group are not consistent and overlap among species. Notably, these include leaf shape (described by blade length/width; all species in this group have the same general shape, so this ratio is an appropriate statistic) and both absolute and relative petiole lengths (Table 3; Figure 1). Although very different species may show no overlap, others, like *A. rhomboidea* and *A. virginica*, show no reliable differences in these characters. Neither is the presence or absence of spreading trichomes on the stems reliable. Nearly 10% of the *A. virginica* specimens I sampled lacked spreading trichomes, whereas 5% of *A. rhomboidea* specimens sampled bore them. Spreading stem trichomes are absent on the remaining species. It is likely that use of these unreliable characteristics has contributed to the relatively frequent misidentifications and the taxonomic confusion in this group.

The data summarized in Table 3 demonstrate that, in fact, intermediates among the taxa in the *Acalypha virginica* group are exceedingly rare or absent. The taxa are often found growing


1.0
0.8
0.6
0.4
0.2
Petiole length/leaf length
2
4
6
8
10
Leaf length/width


14
12
10
8
6
4
Number of carpellate bract lobes
0.0
0.2
0.4
0.6
0.8
Carpellate bract lobe length/bract length

nearby or together, notably *A. deamii* with *A. rhomboidea*; *A. gracilens* with *A. monococca*, *A. rhomboidea*, or *A. virginica*; *A. monococca* with *A. virginica*; and, most frequently, *A. rhomboidea* with *A. virginica* (pers. obs.). Yet examination of over 6500 specimens revealed no clear evidence for hybridization, nor have I found evidence for hybridization during field work throughout much of the range of these taxa.

The presence of unique apomorphies (Table 3) for *Acalypha deamii* (two carpels/flower, seeds at least 2.2 mm long), *A. monococca* (one carpel/flower), and *A. virginica* (long spreading eglandular trichomes on the abaxial surface of the pistillate bracts), supports recognition of these taxa as species under both the phylogenetic (Davis and Nixon 1992; Nixon and Wheeler 1990) and genealogical (Baum and Donoghue 1995; de Queiroz and Donoghue 1988; Olmstead 1995) species concepts. Because they are distinguishable by nonoverlapping characters, *A. gracilens* and *A. rhomboidea* would also be species under the phylogenetic species concept, but because they lack unique apomorphies (insofar as known), they would be metaspecies under the genealogical species concept. In either case, under both of these cladistically based species concepts, all the taxa in the *A. virginica* group should be recognized at the rank of species. I do not recognize any infraspecific taxa in *A. gracilens* because variation in this species is clinal over broad geographic areas (Levin 1998).

**Key to the species of the *Acalypha virginica* group.** I also include in the key the introduced *Acalypha australis*, which may be confused with members of this group.

1. Leaf blades linear to oblong-lanceolate; petioles rarely more than $\frac{1}{4}$ the length of the leaf blades; bracts of pistillate flowers with deltoid teeth $\frac{1}{10}$–$\frac{1}{4}$ length of the bract, with sparse to dense sessile red glands ................ (2)

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←

Figure 1. Plots showing the variation in the *Acalypha virginica* group along four characters. All species are represented by n = 100 except *A. deamii*, a rare species with n = 35. Note that both axes in the upper graph are logarithmic. Key to symbols: *A. deamii* ○, *A. gracilens* □, *A. monococca* ◊, *A. rhomboidea* △, and *A. virginica* ☆.

2. Pistil with 3 carpels, usually producing 3 seeds ..... ................................ *Acalypha gracilens*
2. Pistil with 1 carpel, producing 1 seed .............. ............................. *Acalypha monococca*

1. Leaf blades broadly lanceolate to ovate; petioles more than 1/4 (usually more than 1/3) the length of the leaf blades; bracts of pistillate flowers either with triangular to lanceolate lobes more than 1/4 the length of the bract or with rounded teeth less than 1/10 the length of the bract, lacking red glands ......................................... (3)
    3. Bracts of pistillate flowers hirsute with dense long spreading non-glandular hairs (also ciliate and often with stalked glands), and with (9–) 10–14 (–16) lobes more than 1/4 the length of the bract; stems usually hirsute with long spreading hairs ..... ........................... *Acalypha virginica*
    3. Bracts of pistillate flowers without long spreading non-glandular hairs (may be ciliate or with stalked glands), and with either (5–) 7–9 (–11) lobes more than 1/3 the length of the bract or 12–15 teeth less than 1/10 the length of the bract; stems very rarely hirsute ................................. (4)
        4. Bracts of pistillate flowers with 12–15 rounded teeth less than 1/10 the length of the bract ....... ......................... *Acalypha australis*
        4. Bracts of pistillate flowers with (5–) 7–9 (–11) lanceolate lobes more than 1/3 the length of the bract ...................................... (5)
            5. Pistils with 3 carpels; seeds <2.1 mm long ..... .................. *Acalypha rhomboidea*
            5. Pistils with 2 carpels; seeds >2.1 mm long ..... ...................... *Acalypha deamii*

## Taxonomic treatment of the *Acalypha virginica* group.

1. **Acalypha deamii** (Weath.) H. E. Ahles in Jones & Fuller, Vasc. Pl. Illinois 301. 1955.

*Acalypha virginica* L. var. *deamii* Weath., Rhodora 29: 197. 1927. TYPE: UNITED STATES. Indiana: Dearborn Co., road along White Water River, 2 mi. northeast of Logan, Oct 20, 1924. *C.C. Deam 41107*

(HOLOTYPE: IND!; ISOTYPE: GH!). *Acalypha rhomboidea* Raf. var. *deamii* (Weath.) Weath., Rhodora 39: 16. 1937.

2. **Acalypha gracilens** A. Gray, Manual 408. 1848. TYPE: UNITED STATES. Virginia. *F.I.X. Rugel s.n.* (LECTOTYPE—designated by G. A. Levin, Syst. Bot. 23:285. 1998[1999]: GH!; ISOLECTOTYPE: G). *Acalypha virginica* L. var. *gracilens* (A. Gray) Müll. Arg., Linnaea 34: 45. 1865.

*Acalypha virginica* L. var. *fraseri* Müll. Arg., Linnaea 34: 45. 1865. TYPE: UNITED STATES. South Carolina. *J. Fraser s.n.* (HOLOTYPE: G-DC, microfiche!). *Acalypha gracilens* A. Gray var. *fraseri* (Müll. Arg.) Weath., Rhodora 29: 202. 1927.

*Acalypha gracilens* A. Gray var. *delzii* Lill. W. Miller, Sida 3: 447. 1969. TYPE: UNITED STATES. Arkansas: Hot Spring Co., Bismarck P.O., Jul 14, 1957. *D. Demaree 39432* (HOLOTYPE: SMU!; ISOTYPES: GH!, KANU!, OKL!).

3. **Acalypha monococca** (Engelm. ex A. Gray) Lill. W. Miller & Gandhi, Sida 13: 123. 1988.

*Acalypha gracilens* A. Gray var. *monococca* Engelm. ex A. Gray, Manual, ed. 2, 390. 1856. TYPE: UNITED STATES. Missouri: St. Louis Co., limestone precipices on the banks of the Mississippi River near St. Louis, Sep–Oct 1844. *G. Engelmann s.n.* (HOLOTYPE: GH!; ISOTYPE: WIS!). *Acalypha gracilens* A. Gray ssp. *monococca* (Engelm. ex A. Gray) G. L. Webster, J. Arnold Arbor. 48: 373. 1967.

4. **Acalypha rhomboidea** Raf., New Fl. 1: 45. 1836. TYPE: UNITED STATES. South Carolina. *C.S. Rafinesque s.n.* (LECTOTYPE—designated by C. A. Weatherby, Rhodera 42: 96. 1940: G-DEL, photo at GH!). *Acalypha virginica* L. var. *genuina* Müll. Arg., Linnaea 34: 44. 1865. *Acalypha virginica* L. var. *rhomboidea* (Raf.) Cooperr., Michigan Bot. 23: 165. 1984.

5. **Acalypha virginica** L., Sp. P1. 1003. 1753. TYPE (conserved): UNITED STATES. Virginia. *J. Clayton 201* (HOLOTYPE: BM, drawing at GH!). *Acalypha virginica* L. var. *intermedia* Müll. Arg., Linnaea 34: 45. 1865.

*Acalypha digyneia* Raf., Fl. Ludov. 112. 1817. TYPE: none located.

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DAV, DES, DHL, DS, EIU, F, FARM, FLAS, FSU, FTG, GA, GH, GMUF, IA, ILLS, IND, ISC, KANU, KE, LL, LSU, LYN, MARY, MICH, MIN, MO, MT, MU, NCU, ND, NEB, NEBC, NMC, NY, NYS, OKL, OKLA, OS, PAUH, PENN, PH, POM, PUL, RSA, SD, SMU, TAES, TAIC, TENN, TEX, TRT, UARK, UC, UNA, UNC, UNM, US, USCH, USF, VP, VPI, VT, WILLI, WIS, and WVA. Rick Phillippe, Steve Hill, Tom Mione, and two anonymous reviewers provided helpful comments on earlier versions of the manuscript.

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# THE FRESHWATER SPECIES OF *VAUCHERIA* (TRIBOPHYCEAE, CHRYSOPHYTA) FROM CONNECTICUT

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ABSTRACT. Having scoured freshwater habitats throughout Connecticut for more than two years at 151 collection sites, we have discovered the presence of nine species and two varieties of the genus *Vaucheria*, including four species not previously known from the state: *V. prona*, *V. taylorii*, *V. uncinata*, and *V. undulata*. In addition, *V. compacta*, normally found in local estuaries, is reported in freshwater here, and is distinguished from its local freshwater variety, *V. compacta* var. *dulcis*. Culture conditions in the laboratory stimulated production of gametangia, allowing for identification of mostly vegetative field-collected samples. A key to the species and varieties is provided.

Key Words: *Vaucheria*, Vaucheriaceae, Tribophyceae, Connecticut

*Vaucheria* is a yellow-green alga commonly encountered along freshwater stream and river banks, in mud surrounding small ponds and marshes, in drainage ditches alongside roadways, and in puddles and vernal pools worldwide. In habitats such as these, coenocytic siphons of *Vaucheria* act as ecologically important substratum stabilizers, often during continual environmental disruption. Although most species in the genus live in freshwater, several species are found in brackish water, and a few are completely restricted to marine environments (Blum 1972). *Vaucheria* species have been shown to be euryhaline, often tolerating great variation in salinity in very short periods of time (Schneider et al. 1993).

The first recorded collections of freshwater *Vaucheria* from Connecticut were included in the early and important North American exsiccata, *Phycotheca Boreali-Americana* (*P.B.-A.*, Collins et al. 1895, 1898, 1905). This exsiccata included three freshwater *Vaucheria* specimens from the state: *V. terrestris* Lyngb. [= *V. frigida* (Roth) C. Agardh], Fasc. II (1895), no. 78a

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(*Setchell*, 9.x.1892, Norwich); *V. aversa* Hassall, Fasc. X (1898), no. 475 (*Holden*, 3.xiii.1892, Mill R., Fairfield); and *V. geminata* (Vaucher) DC with some *V. geminata* var. *racemosa* (Vaucher) Walz [= *V. racemosa* (Vaucher) DC], Fasc. XXVI (1905), no. 1287, (*Holden*, 9.iv.1892, Ash Creek, Bridgeport). In his monographic treatment of freshwater and marine "green" algae from North America, Collins (1909) included only five freshwater species of *Vaucheria* for all of North America, reflecting the limited knowledge of the genus at that time. Of these, only *V. aversa* and *V. sessilis* (Vaucher) DC [= *V. bursata* (O. F. Müll.) C. Agardh] were reported from Connecticut. Conn and Webster (1908) published the first report on freshwater algae specifically from the state, and recorded only one species, *V. bursata* (as *V. sessilis*). Hylander (1925, 1928) included five freshwater species of *Vaucheria* in his "Algae of Connecticut," based on limited reports from throughout the state. These included *V. aversa* from Fairfield; *V. bursata* (as *V. sessilis*) from Brookfield and Middletown; *V. frigida* (as *V. terrestris*) from Litchfield, Hartford, New Haven, and New London counties; *V. geminata* from Bridgeport, Barkhamsted, and New Haven; and *V. racemosa* (as *V. geminata* var. *racemosa*) from New Haven (Hylander, 1925). Each of these species was then recorded in the first monograph of *Vaucheria* for North America by Helen Brown (1929). John Blum's (1972) later seminal monograph on the "Family Vaucheriaceae," published as part of the New York Botanical Garden's "North American Flora," included 22 freshwater and 20 marine species, but none with specific reference to the state. Since 1928, only one species has been added to the freshwater *Vaucheria* flora of Connecticut, when *V. compacta* var. *dulcis* J. Simons was found in abundant populations near the junction of the Farmington and Connecticut Rivers (Schneider et al. 1996).

Thus, in the more than a century since the first reports of *Vaucheria* from Connecticut in *P.B.-A.*, only six freshwater species have been reported. During this time, collections were made from only a few localities, mostly in the western part of the state, and only a few sites were visited throughout the year. Considering that fourteen freshwater species have been reported for New England, New York, and New Jersey (Blum 1972), not including one presently known only from Connecticut within that range (*V. compacta* var. *dulcis*), the timing seemed right to conduct a basic field and laboratory study to assess the diversity of freshwater

*Vaucheria* in the state, and to broadly survey the local species distributions. Only four marine/brackish species of *Vaucheria* from Connecticut were recorded prior to a similar coastal study of the genus, and five species and one variety were subsequently added to the local flora after extensive field and culture work (Schneider et al. 1993).

## MATERIALS AND METHODS

Since the initiation of this study in 1994, we have visited 151 riparian and limnic habitats, muddy wetlands, drainage ditches, and roadside catchments, often revisiting the same sites in different seasons. Crude samples were collected either as siphonous algal mats attached to substratum, or mud itself with no obvious signs of *Vaucheria.* Using a flat spatula, substrata were cut into approximate 100 $cm^2$ quadrats, varying in thickness from 2–3 cm. At the site, after temperature was recorded for proximal standing water, pH (Corning pH 103 meter) and salinity were measured (Reichert-Jung refractometer 11719-2). Field evaluation of the substratum type (sand, mud, etc.) was made. Codes identifying the collecting sites are given in the Appendix (bold face), and numbers at the end of codes under "REPRESENTATIVE COLLECTIONS" represent the first, second, third, etc. visit/collection in the same location. Collection data are followed by the first date of gametangia appearance in culture, or noted if they were fertile in the field collection.

The crude samples were collected in labeled, zippered, plastic bags and transported on ice to the laboratory where they were immediately subdivided into three labeled culture dishes. Vascular plants, sticks, and leaves were removed from the surface. Bold's basal medium (Bischoff and Bold 1963) was added to each culture dish to a depth of approximately one-third the thickness of the crude sample. Samples were distributed among three photoperiods (8L:16D, 12L:12D, 16L:8D) in Hotpack incubators (#352642) set at 15°C, an optimum temperature for the growth of *Vaucheria* (Schneider et al. 1993). Microscopical observations on each crude culture were made every five to ten days. Drawings were made with the aid of a Zeiss camera lucida, and microscope slide vouchers (20% or 40% Karo™ corn syrup, 1% aniline blue in 1N HCl in a ratio of 20:1:1) are deposited in Herbarium/C. W. Schneider at Trinity College. The *P.B.-A.* set utilized in the present study was originally purchased by Wellesley College (Fahey and Doty 1955) and is presently located in the Herbarium/C. W. Schneider. Standard forms of author names follow Brummitt and Powell (1992). Because other works (e.g., Blum 1972; Entwisle 1988a) include world distributions for the species found in Connecticut and are often not specific for a particular place, citing "widespread in North America," we have listed states and provinces in the northeastern part of North America with known reports under the designation "NORTHEAST DISTRIBUTION."

## RESULTS AND DISCUSSION

Few samples collected were fertile in the field. The remainder of the collections with obvious *Vaucheria* siphons later produced gametangia after 10–14 days in culture, on the average. About 30% of the mud samples never produced *Vaucheria* after incubation in culture media. In others without obvious *Vaucheria*, either siphons existed within the mud below grade, or dormant zygotes or asexual spores were coaxed into germinating under favorable culture/incubator conditions. Many cultures produced two to six biotic sympatric species over time in a single crude sample. Most species discovered in this study presented unremarkable features from those reported for other North American populations, so the reader is referred to Blum (1972) for full descriptions including pertinent measurements. Where our observations have been at variance with Blum (1972), these are noted below. We have discovered great variability in our extensive collections, allowing for a greater understanding of the species and overlap among them. Thus, when working with the polymorphic *Vaucheria*, it is advisable to sample widely for species and to rely on measurements and morphological characteristics of many individuals before making taxonomic determinations.

Although we have sampled extensively throughout the state, we have the fewest *Vaucheria* species records (four) from the northwestern Litchfield Co. This is in part due to more limited sampling there (14 sites), but mostly because of the poor, often sandy, substrata found in this part of the state. New records for Connecticut are noted with asterisks (*).

## VAUCHERIACEAE Dumortier 1822, p. 71

*Vaucheria aversa* Hassal 1843, p. 429. Figures 1–3, 46.

TYPE LOCALITY: vic. Chestnut, England.

NORTHEAST DISTRIBUTION: Maine, N.H., Mass., Conn., N.Y., N.J.

REPRESENTATIVE COLLECTIONS: Fairfield Co.—**KP1**, *CEL*, coll. 25.x.1998, gam. 1.xi.1998; **NR2**, *CEL*, coll. 28.xi.1997, gam. 7.ii.1998; **PB1**, *CEL*, coll. 28.xi.1997, gam. 6.i.1998; **PN1**, *CEL*, coll. 31.v.1998, gam. 6.vi.1998; **SNR1**, *CEL*, coll. 25.x.1998, gam. 1.xi.1998. Hartford Co.—**BBB2**, *CWS*, coll. 10.xii.1997, gam. 6.i.1998; **BRWB**, *CWS*, coll. 12.xii.1997, gam. 23.v.1998; **CP1**, *AN*, coll. 22.ii.1998, gam. 23.v.1998; **EGST**, *CWS*, coll. 12.xii.1997, gam. 3.iii.1998; **GMS1**, *CEL/CWS*, coll. 5.vi.1998, gam. 14.vi.1998; **GRDD1**, *AN*, coll. 22.ii.1998, gam. 22.iv.1998; **JB1**, *AN*, coll. 22.ii.1998, gam. 28.v.1998; **LJB1**, *AN*, coll. 22.ii.1998, gam. 28.v.1998; **PGB1**, *CEL*, coll. 10.x.1997, gam. 22.iv.1998; **SBBB1**, *CEL*, coll. 21.x.1997, gam. 29.xi.1997; **SCR1**, *CEL/CWS*, coll. 5.vi.1998, gam. 31.ix.1998. Middlesex Co.—**SR2**, *CWS*, coll. 28.ix.1997, gam. 23.xii.1997. New Haven Co.—**DLF1**, *AN/CEL*, coll. 15.xi.1997, gam. 13.i.1998; **EMR1**, *AN/CEL*, coll. 3.xii.1997, gam. 3.iii.1998. New London Co.—**AR1**, *CEL*, coll. 23.v.1998, gam. 7.vii.1998; **BBS1**, *CWS*, coll. 29.xi.1997, gam. 3.ii.1998; **LBM1**, *CWS*, coll. 29.xi.1997, gam. 13.i.1998; **LEL1**, *CWS*, coll. 29.xi.1997, gam. 10.iii.1998; **ST1**, *CEL*, coll. 23.v.1998, gam. in field. Tolland Co.—**AB1**, *CWS/AN*, coll. 12.iii.1998, gam. 25.v.1998; **CB1**, *CEL*, coll. 30.vii.1998, gam. 10.x.1998; **SKR1**, *CEL*, coll. 11.xi.1997, gam. 12.i.1998. Windham Co.—**NK1**, *AN/CWS*, coll. 18.ix.1997, gam. 21.v.1998; **NK7**, *MED/CWS*, coll. 29.ix.1998, gam. 22.x.1998; **QR1**, *CEL*, coll. 20.viii.1998, gam. 31.ix.1998.

REMARKS. *Vaucheria aversa* was first reported for Connecticut in *P.B.-A.* by Collins et al. (1898) and later by Hylander (1925, 1928). Blum (1972) reported this species in eastern and midwestern United States and Alaska. We have found *V. aversa* throughout Connecticut (Figure 46) in river beds, drainage ditches, and woodland trails—this species appeared in 20% of our crude cultures. Often, samples containing this species did not appear as fertile siphons until two or more months in culture. In a few instances, after being in culture for up to 3 months, *V. aversa* became the dominant species in the crude samples, excluding others.

*Vaucheria aversa* is one of two species in Connecticut, along with *V. bursata*, with sessile gametangia. These two can be easily distinguished by the angle and appearance of oogonia and by antheridial morphology. Oogonia of *V. bursata* have completely-filled cavities at maturity and have beaks that are directed at 70–80° angles from the siphons towards the adjacent long, curled, cylindrical antheridia (Figures 4–8). The oogonia of *V. aversa* have peripheral cavities when mature and arise at 20–30° angles, with their beaks deflected downwards to the siphons in the vicinity of the adjacent short, straight, fusiform to cylindrical antheridia (Figures 1–3). Neither of these two could be confused with any other freshwater Connecticut species.

*Vaucheria bursata* (O. F. Müll.) C. Agardh 1811, p. 21.
Figures 4–8, 47.

BASIONYM: *Conferva bursata* O. F. Müll. 1788, p. 96.
TYPE LOCALITY: Geneva, Switzerland.
NORTHEAST DISTRIBUTION: Maine, Mass., R.I., Vt., Conn., N.J.

REPRESENTATIVE COLLECTIONS: Fairfield Co.—**CD1**, *CEL*, coll. 31.v.1998, gam. 28.vi.1998; **CPG1**, *CEL*, coll. 31.v.1998, gam. 6.vi.1998; **KP1**, *CEL*, coll. 25.x.1998, gam. 28.x.1998; **NB1**, *CEL*, coll. 28.xi.1997, gam. 12.i.1998; **NCM1**, *CEL*, coll. 25.x.1998, gam. in field; **MB1**, *CEL*, coll. 28.xi.1997, gam. 3.iii.1998; **PN1**, *CEL*, coll. 31.v.1998, gam. 6.vi.1998; **WMR1**, *CEL*, coll. 25.x.1998, gam. in field. Hartford Co.—**BBB1**, *CWS*, coll. 10.xii.1997, gam. 20.i.1998; **BRWB1**, *CWS*, coll. 12.xii.1997, gam. 27.v.1998; **BUR1**, *CWS/CEL*, coll. 5.vi.1998, gam. in field; **FTS1**, *CWS*, coll. 21.ix.1994, gam. 24.iv.1996; **GSB1**, *CWS*, coll. 12.xii.1997, gam. 3.ii.1998; **NH1**, *CEL*, coll. 8.x.1997, gam. 23.x.1997; **PGB1**, *CEL*, coll. 10.x.1997, gam. 17.x.1997; **RGB1**, *CEL/CWS*, coll. 5.vi.1998, gam. 14.vi.1998; **RP2**, *AN*, coll. 13.xi.1997, gam. 29.xi.1997; **TMR1**, *AN/CEL*, coll. 1.x.1997, gam. 14.x.1997; **WBB1**, *CWS*, coll. 10.xii.1997, gam. 25.v.1998; **WHR1**, *AN*, coll. 13.xi.1997, gam. 2.xii.1997; **WPF2**, *AN*, coll. 7.x.1997, gam. 31.x.1997. Litchfield Co.—**BBR1**, *CEL*, coll. 30.vii.1998, gam. 3.ix.1998; **BNB1**, *CEL*, coll. 1.ix.1998, gam. 29.ix.1998; **EA1**, *CEL*, coll. 1.ix.1998, gam. in field; **HOR2**, *CEL*, coll. 30.vii.1998, gam. 21.ix.1998; **KFB1**, *CEL*, coll. 30.vii.1998, gam. 12.xi.1998; **NCWR1**, *CEL*, coll. 30.vii.1998, gam. 23.ix.1998. New London Co.—**LBM1**, *CWS*, coll. 29.xi.1997, gam. 24.vi.1998; **ST1**, *CEL*, coll. 23.v.1998, gam. in field; **TR2**, *AN/CEL*, coll. 22.x.1997, gam. 1.xi.1997. Tolland Co.—**SKR2**, *CEL*, coll. 23.v.1998, gam. 9.ix.1998.

REMARKS. *Vaucheria bursata* was first reported in Connecticut as *V. sessilis* (Vaucher) DC (Lamarck and de Candolle 1805) by Hylander (1928) and Brown (1929). *Vaucheria sessilis* was shown by Christensen (1973) to be a junior synonym of *V. bursata*, based upon Müller's (1788) illustrations of *Conferva bursata*, as well as collections Christensen made at Bad Meinberg, southwest of Hanover, Germany. Blum (1972) maintained *V. ses-*

*silis* and two similar species, *V. repens* Hassall and *V. clavata* sensu Klebs, differentiating each by siphon diameter and number of oogonia in association with each antheridium. Based upon our collections of *V. bursata* from a variety of habitats in Connecticut, we find these distinctions untenable, and follow Entwisle (1987, 1988a) in considering these as heterotypic synonyms of *V. bursata*. For example, we have found individual siphons with one and two oogonia associated with an antheridium. Our collections of this cosmopolitan freshwater species come from all but two counties in the state, Middlesex and Windham (Figure 47). *Vaucheria bursata* appeared in 20% of our crudes cultures, thus being one of the most commonly encountered species in the state.

*Vaucheria compacta* var. *compacta* (Collins) Collins ex W. R. Taylor 1937, p. 226. Figures 9–11, 48.

BASIONYM: *Vaucheria piloboloides* var. *compacta* Collins 1900, p. 13.

TYPE LOCALITY: Malden Mass., United States.

NORTHEAST DISTRIBUTION (freshwater only): Conn.

COLLECTIONS: Fairfield Co.—**CD1**, *CEL*, coll. 31.v.1998, gam. 6.vi.1998; **BPG1**, *CEL*, coll. 31.v.1998, gam. 6.vi.1998.

REMARKS. This species is widespread in New England saltmarshes (Blum and Conover 1953) and was first reported in Connecticut as *Vaucheria piloboloides* by Collins (1900). In our study of brackish and saltwater species in Connecticut, we commonly found *V. compacta* throughout the northern coast of Long Island Sound (Schneider et al. 1993). In cultures from these coastal areas, we found *V. compacta* growing and fertile from 0.3–30‰ salinity. This species is only known from very low salinity *in situ* brackish water in Louisiana (2.2‰; Pecora 1977), and elsewhere can be found in supersaline environments (Christensen 1987, 1988; Simons 1974). Our "freshwater" collections of *V. compacta* from Greenwich (Figure 48) are from two sites where the *in situ* salinity was 1‰ and 2‰, comparable to the levels recorded for this species in Louisiana (Pecora 1977)—sites where *V. undulata* and *V. bursata*, two other freshwater species, were found. These are the first low-salinity collections from the northeast other than the records of its freshwater variety, *V. compacta* var. *dulcis* (see below).

*Vaucheria compacta* is dioecious. After a month in freshwater culture, both samples produced male gametangia only in the 16L/8D photoperiod regime, with the samples in 8L/16D and 12L/12D remaining vegetative. The antheridia were mostly of the typical "brackish-type," with two or more lateral discharge pores (Figures 9, 10), not to be confused with those produced by *V. compacta* var. *dulcis* that have one or no lateral discharge pores (Figures 12, 13) (Schneider et al. 1996; Simons 1974). In both Greenwich samples, the siphons produced male gametangia for less than two weeks. Thereafter the cultures became overgrown by other freshwater algal species including *Vaucheria.*

*Vaucheria compacta* var. *dulcis* J. Simons 1974, p. 624.
Figures 12, 13, 49.

TYPE LOCALITY: The Netherlands.
NORTHEAST DISTRIBUTION: Conn., Delaware.

REPRESENTATIVE COLLECTIONS: Hartford Co.—**RPC**, *CWS*, coll. 8.x.1992, gam. 21.x.1992; **FW**, *CWS*, coll. 8.x.1992, gam. 26.x.1992; **FP2**, *CEL/CWS*, coll. 5.vi.1998, gam. 24.vi.1998.

REMARKS. Despite our extensive collections of *Vaucheria* in the state during all seasons over two years, we have not located this freshwater variety of *V. compacta* in locations outside those in the original report for North America of dense year-round populations in the Connecticut and Farmington Rivers below the Rainbow Dam (Figure 49; Schneider et al. 1996). These populations remain present and abundant only in areas of the Farmington River where they receive daily "hydrotidal" flooding from the twice-daily hydroelectrical generation produced by the dam, as well as natural tidal effects from Long Island Sound in the Connecticut River. Schneider et al. (1996) speculated that the variety's exclusive distribution in Connecticut would be only to areas receiving daily freshwater tidal flushing and this has been borne out by a lack of collections from sites other than those in the original report. We cannot speculate why this variety hasn't found its way to the lower Housatonic and Thames River systems, as both are affected by tidal waters. In the Farmington River, *V. compacta* var. *dulcis* thrives as thick continuous mat-like bands, especially along the banks with the greatest flow of water, and unlike other *Vaucheria* species in the state, it seems to grow to the exclusion of other species (Schneider et al. 1996).

Despite years of culture work and field collections, we have yet to find or produce oogonia on plants from these sites, though antheridia have been abundant (Schneider et al. 1996). Nevertheless, differences in the antheridial morphology allowed us to differentiate this European variety from the nominate species, *Vaucheria compacta*. The freshwater variety maintains its distinctive antheridial characteristics despite drastic salinity changes *in vitro* (Schneider et al. 1996).

*Vaucheria frigida* (Roth) C. Agardh 1824, p. 173.
Figures 14–19, 50.

BASIONYM: *Conferva frigida* Roth 1797, p. 166.

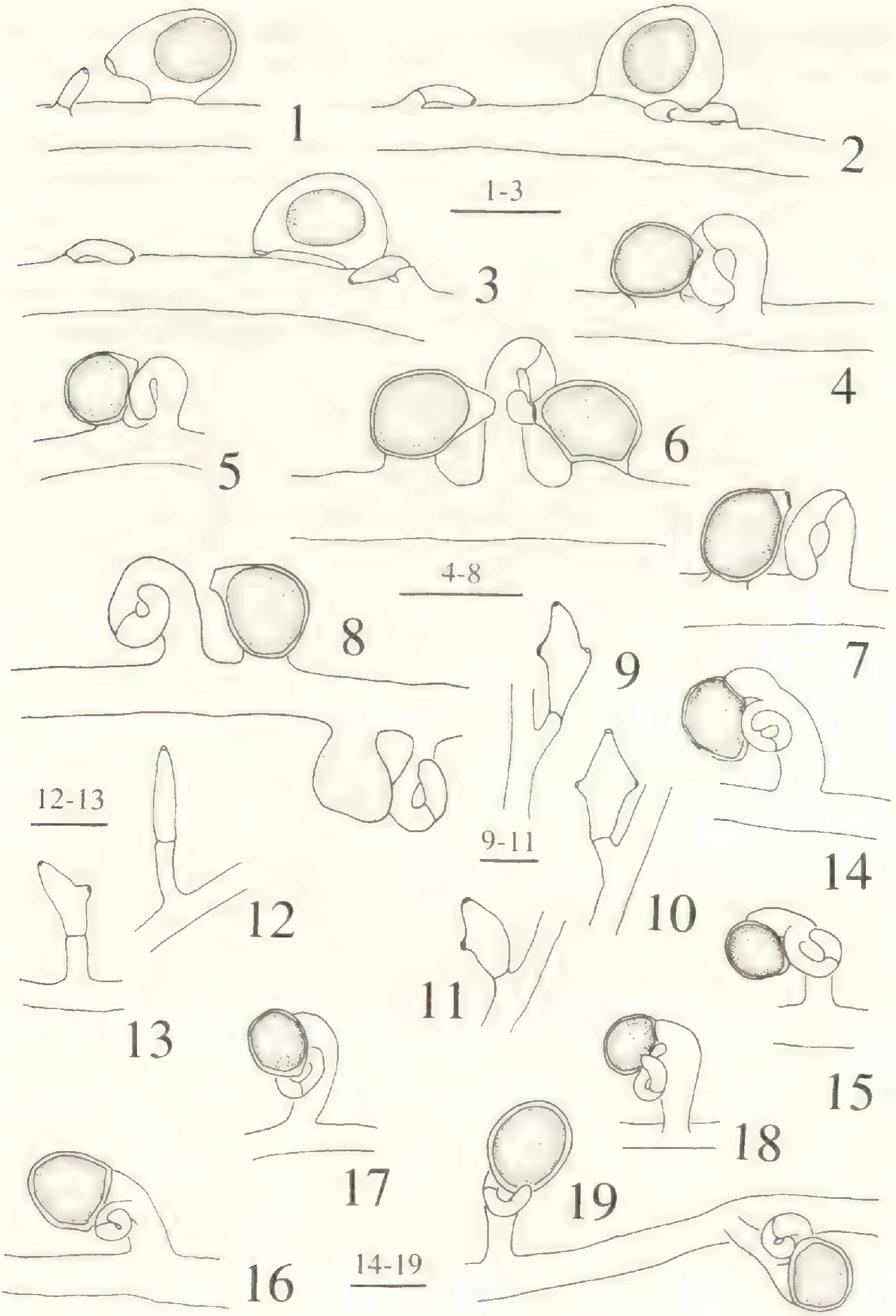
TYPE LOCALITY: London, England.

NORTHEAST DISTRIBUTION: N.B., Maine, Mass., R.I., Conn., N.Y.

REPRESENTATIVE COLLECTIONS: Fairfield Co.—**CPG1**, *CEL*, coll. 31.v.1998, gam. 12.xi.1998; **MB1**, *CEL*, coll. 28.xi.1997, gam. 3.ii.1998; **NR2**, *CEL*, coll. 28.xi.1997, gam. 6.xii.1997; **PB1**, *CEL*, coll. 28.xi.1997, gam. 6.i.1998. Hartford Co.—**BBB2**, *CWS*, coll. 10.xii.1997, gam. 6.i.1998; **BUR1**, *CWS/CEL*, coll. 5.vi.1998, gam. 2.vii.1998; **FS1**, *CWS*, coll. 5.ix.1995, gam. 10.x.1995; **JB1**, *AN*, coll. 22.ii.1998, gam. 28.v.1998; **RGB2**, *CEL/CWS*, coll. 5.vi.1998, gam. 17.vii.1998; **WP2**, *AN*, coll. 7.x.1997, gam. 29.xi.1997. New London Co.—**SDD1**, *CWS*, coll. 29.xi.1997, gam. 3.i.1998. Tolland Co.—**RRB1**, *CEL*, coll. 6.xi.1997, gam. 25.v.1998. Windham Co.—**LR1**, *CEL*, coll. 20.viii.1998, gam. 12.xi.1998; **NK3**, *AN/CWS*, coll. 18.ix.1997, gam. 29.xi.1997.

REMARKS. For much of its taxonomic history, *Vaucheria frigida* was confused with another species originally described from Europe, *V. terrestris* (Vaucher) DC (Christensen 1968). Early North American collectors apparently followed the account of *V. terrestris* by Götz (1897), a taxon now considered distinct from true *V. terrestris* (Blum 1972; Christensen 1968). Thus, early collections of *V. frigida* from Connecticut were reported as *V. terrestris* (Blum 1953; Brown 1929; Hylander 1925, 1928), as well as distributed in the *P.B.-A.* exsiccata (Collins et al. 1895, no. 78a). *Vaucheria frigida* occurs throughout North America, as well as being cosmopolitan elsewhere, while *V. terrestris* is presently recognized only from Europe (Blum 1972). We have collected *V. frigida* in all seven Connecticut counties, and it appeared in 13% of our cultures (Figure 50).

In *Vaucheria frigida*, thick-walled oogonia are borne singly on fruiting branches distal to single circinate antheridia. Long axes of oogonia are projected either horizontally or directed back at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Figures 1–19. Connecticut freshwater *Vaucheria* species. 1–3. *V. aversa*; 4–8. *V. bursata*; 9–11. Antheridia of *V. compacta* var. *compacta*; 12–13. Antheridia of *V. compacta* var. *dulcis*; 14–19. *V. frigida*. All scale bars = 100 μm.

the supporting siphons bearing fruiting branches (pedicels). The species can be confused with single oogonial forms of *V. undulata*, but there are obvious differences between the two, not the least of which are the spiraled siphons of the latter (see below). Blum (1972) found considerably larger oogonia in *V. frigida* (80–135 × 106–165 μm) than in *V. undulata* (71–113 × 96–127 μm). Our collections as well yielded larger oogonia for *V. frigida* (81–110 × 93–140 μm) than for *V. undulata* (50–80 × 60–100 μm), but these had somewhat smaller dimensions than those listed by Blum (1972). While *V. undulata* often bears reproductive branches with a single oogonium, rarely are there vegetative siphons without reproductive branches bearing two oogonia. As siphons of *V. undulata* mature and bear more gametangia, the pedicels usually proliferate from one another, a phenomenon only observed once in eighteen fertile collections of *V. frigida*, and not nearly to the extent of that seen in *V. undulata* (see below).

*Vaucheria geminata* (Vaucher) DC in Lamarck et DC 1805, p. 62. Figures 20–22, 51.

BASIONYM: *Ectosperma geminata* Vaucher 1803, p. 29.

TYPE LOCALITY: Between Geneva and Versoix, Switzerland.

NORTHEAST DISTRIBUTION: Maine, N.H., Vt., Mass., Conn., N.J.

REPRESENTATIVE COLLECTIONS: Fairfield Co.—**BSP1**, *CEL*, coll. 31.v.1998, gam. 6.vi.1998; **BUR1**, *CEL/CWS*, coll. 5.v.1998, gam. 28.vi.1998; **NB1**, *CEL*, coll. 28.xi.1997, gam. 25.v.1998; **PB1**, *CEL*, coll. 28.xi.1997, gam. 22.iv.1998. Hartford Co.—**EGST**, *CWS*, coll. 12.xii.1997, gam. 3.ii.1998; **GMS1**, *CEL/CWS*, coll. 5.vi.1998, gam. 14.vi.1998; **LJB1**, *AN*, coll. 22.ii.1998, gam. 14.iv.1998; **LV1**, *CEL*, coll. 21.x.1997, gam. 29.xi.1997; **NBBB1**, *CWS*, coll. 8.xi.1997, gam. 3.i.1998; **NH1**, *CEL*, coll. 8.x.1997, gam. 23.x.1997; **QP1**, *AN/CEL*, coll. 1.x.1997, gam. 22.iv.1998; **SCR1**, *CEL/CWS*, coll. 5.vi.1998, gam. 14.vi.1998; **WHR1**, *AN*, coll. 13.xi.1997, gam. 2.xii.1997. Litchfield Co.—**HOR2**, *CEL*, coll. 30.vii.1998, gam. 20.xi.1998. Middlesex Co.—**SR2**, *CWS*, coll. 28.ix.1997, gam. 11.x.1997. New London Co.—**CCR1**, *CEL*, coll. 23.v.1998, gam. 6.vi.1998; **LBM1**, *CWS*, coll. 29.ix.1997, gam. 16.ii.1998; **SDD1**, *CWS*, coll. 29.ix.1997, gam. 22.iv.1998; **ST1**, *CEL*, coll. 23.v.1998, gam. 14.vi.1998. Windham Co.—**NK3**, *AN/CWS*, coll. 18.ix.1997, gam. 15.x.1997.

REMARKS. Collins et al. (1905) first reported *Vaucheria geminata* from Connecticut, followed by the reports of Hylander (1925, 1928), and in this study it was collected in 18% of our samples from throughout the state (Figure 51).

*Vaucheria geminata* almost invariably produces two opposite oogonia on short to slightly extended pegs off erect reproductive branches at abaxial angles of 50–70° (Figures 21, 22). In a few instances, we found reproductive branch proliferation (Figure 20), a phenomenon also noted by Christensen (1969; fig. 9837a, i) for *V. geminata*. The oogonia are ovoid to slightly reniform in shape (Figures 20–22) and range from 60–78 × 62–90 μm. Circinate antheridia are borne singly and terminally in between and distal to the oogonia, but mostly not projecting beyond the height of the oogonia (Figures 20–22). Fertile *V. geminata* appear very similar to forms of *V. taylorii* that bear two oogonia on reproductive branches (see below), with the distinguishing characters of not-overly-swollen pedicels (often distinctly swollen in *V. taylorii*) and the height of antheridia (*V. taylorii* mostly has its antheridia exceeding the tops of the oogonia on pedicels). Oogonia are often distinctly flattened on adaxial surfaces in *V. taylorii* (see below), a characteristic not seen in *V. geminata*. As discussed later in this report, the Connecticut specimens of *V. geminata* and its var. *racemosa* distributed in *P.B.-A.* (XXVI:1287), are now seen to be a polymorphic collection of *V. taylorii*.

**Vaucheria prona* T. A. Chr. 1970, p. 250. Figures 23–27, 52.
TYPE LOCALITY: Kongelunden, Amager, Denmark.
NORTHEAST DISTRIBUTION: Mass., Conn., N.Y.

REPRESENTATIVE COLLECTIONS: Fairfield Co.—**BSP1**, *CEL*, coll. 31.v.1998, gam. 6.vi.1998; **NR2**, *CEL*, coll. 28.ix.1997, gam. 6.xii.1997; **PB1**, *CEL*, coll. 28.ix.1997, gam. 22.iv.1998; **SNR1**, *CEL*, coll. 25.x.1998, gam. in field. Hartford Co.—**BBB1**, *CWS*, coll. 10.xii.1997, gam. 2.iii.1998; **CP1**, *AN*, coll. 22.ii.1998, gam. 3.xi.1998; **GRDD1**, *AN*, coll. 22.ii.1998, gam. 22.iv.1998; **HLM**, *CWS*, coll. 23.xi.1998, gam. in field; **JB1**, *AN*, coll. 22.ii.1998, gam. 28.v.1998; **LV1**, *CEL*, coll. 21.x.1997, gam. 3.xi.1997; **PGB1**, *CEL*, coll. 10.x.1997, gam. 21.v.1998; **PBW**, *CWS*, coll. 5.xii.1997, gam. 3.i.1998; **QP1**, *AN/CEL*, coll. 1.x.1997, gam. 1.x.1997; **SBBB1**, *CEL*, coll. 21.x.1997, gam. 20.xi.1997; **TMR1**, *AN/CEL*, coll. 1.x.1997, gam. 13.x.1997; **WCP1**, *AN*, coll. 22.ii.1998, gam. 14.iv.1998. New London Co.—**BBS1**, *CWS*, coll. 29.xi.1997, gam. 3.ii.1998; **RRD1**, *AN/CEL*, coll. 22.x.1997, gam. 11.ix.1997; **TR1**, *AN/CEL*, coll. 22.x.1997, gam. 28.x.1997. Tolland Co.—**SKR2**, *CEL*, coll. 23.v.1998, gam. 28.vi.1998. Windham Co.—**NK3**, *AN/CEL*, coll. 18.ix.1997, gam. 29.xi.1997.

REMARKS. Previously encompassed under *Vaucheria terrestris* (Vaucher) DC (=*V. frigida*), Christensen (1970) separated *V. prona* from it, as the former had only a single pendent oogonium on a fertile branch. He noted that his paired, pendent oogonial plants actually represented what was later called *V. hamata* sensu Götz (1897). In order to avoid continued taxonomic confusion, *V. prona* was established as a new species to accomodate this paired oogonial alga rather than reintroducing new concepts for long-established taxa (Christensen 1970). This common alga was designated by early North American workers as *V. hamata*, and is now recognized from collections from throughout the world (Entwisle 1988a). Our isolates of *V. prona* represent the first records of this species from Connecticut, and only the second from New England. This species was found in 16% of our samples, but not in Litchfield, New Haven, and Middlesex counties (Figure 52).

Oogonia on *Vaucheria prona*, like those of *V. frigida*, are formed distally to single antheridia on fertile branches, and are pendent on downwardly curved pegs off curved fertile branches. In some cultures, gametangia were formed terminally on the siphons themselves or on greatly extended fruiting branches. In *V. prona* there are usually two large oogonia (42–68 × 55–78 μm) found on each fruiting branch, and when fully mature have oppositional tips (Figures 24, 26). Occasionally, we have found fruiting branches proliferating from others, while retaining two oogonia on the basal fruiting branch. Such occurrences are not nearly as common as those in *V. undulata*, a species that normally retains only a single oogonium on the basal branch. At one site (**HLM**), we often found *V. prona* producing three or four oogonia per pedicel (Figure 23), and in rare instances, we have found siphons producing only a single oogonium on a fertile branch (Figure 25). The multiple oogonial form is easily distinguished from *V. taylorii* by its pendent oogonia, a phenonmenon also nicely illustrated in Australian populations of this species (Entwisle 1988a; figs 85, 90). However, the single oogonial form of *V. prona* is difficult to distinguish from the single forms of *V. frigida* and *V. undulata*. Careful observations of large populations of *V. frigida* and *V. prona* allow for the separation of the single from paired oogonial species, as the presence of two oogonia in *V. frigida* or one in *V. prona* are infrequent at best. *Vaucheria prona* can be confused with *V. undulata* when the latter species is immature, producing oppositely paired oogonia on reproductive branches. *Vaucheria undulata*, however, has trademark spiraled siphons (Figure 39) and, at maturity, consistently produces proliferating pedicels from the sites where one oogonium in an opposite pair would have formed on a reproductive branch (see below). *Vaucheria prona* can be distinguished from the other local species with opposite oogonia, *V. geminata*, as this species has erect oogonia on straight reproductive branches (Figures 20–22; Entwisle 1988b).

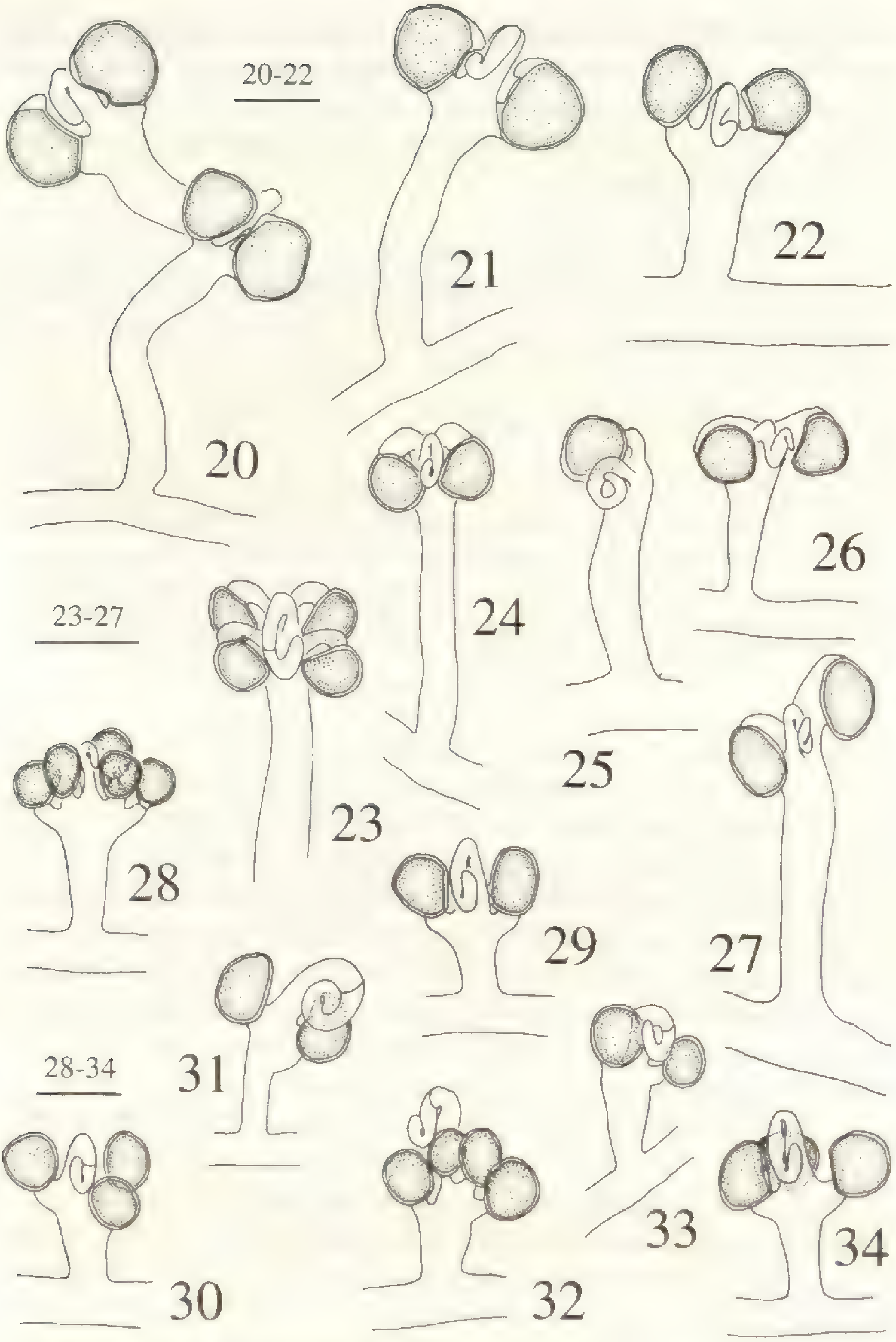
**Vaucheria taylorii* Blum 1971, p. 191. Figures 28–34, 53.

TYPE LOCALITY: Beaver Is., Charlevoix Co., Mich., United States.

NORTHEAST DISTRIBUTION: Maine, Conn.

COLLECTIONS: Fairfield Co.—**KP1**, *CEL*, coll. 25.x.1998, gam. in field; **NB1**, *CEL*, coll. 28.xi.1997, gam. 12.i.1998. Hartford Co.—**BUR1**, *CEL/CWS*, coll. 5.v.1998, gam. 29.vii.1998; **FTS1**, *CWS*, coll. 21.ix.1994, gam. 5.x.1994; **GSB2**, *CWS/CEL*, coll. 5.vi.1998, gam. 11.ix.1998; **NRS1**, *CWS/CEL*, coll. 5.x.1998, gam. 30.xi.1998; **WP1**, *AN*, coll. 7.x.1997, gam. 14.x.1997. Litchfield Co.—**EA1**, *CEL*, coll. 1.ix.1998, gam. 24.x.1998; **HOR2**, *CEL*, coll. 30.viii.1998, gam. 21.ix.1998; **KFB1**, *CEL*, coll. 30.viii.1998, gam. in field; **NN1**, *CEL*, coll. 1.ix.1998, gam. 21.ix.1998. New London Co.—**ST1**, *CEL*, coll. 23.v.1998, gam. 14.vi.1998.

REMARKS. Although our recent collections represent the first report of this species from Connecticut, specimens of *Vaucheria taylorii* were actually distributed in *P.B.-A.* (Collins et al. 1905) as *V. geminata* (Ash Creek, Bridgeport, Conn., *Holden* 9.iv.1892, no. 1287). Collins et al. (1905) noted that this dried specimen contained "mostly the type [of *V. geminata*], but with some var. *racemosa*," this being the sole basis for Hylander's (1928) report of *V. geminata* var. *racemosa* [=*V. racemosa* (Vaucher) DC], a species we have not found in our extensive collections here. We have examined this exsiccata and have established that specimen no. 1287 represents a collection of *V. taylorii* with 2–6 oogonia on fertile branches rather than the two species proposed in the exsiccata. Also, as will be shown below, the illustration of *V. geminata* in Hylander (1928; pl. XX, Fig. 8), could possibly represent *V. taylorii* depending upon the other reproductive branches that may have been associated with it in its original population. The oogonia of *V. taylorii* are borne at erect angles on pegs from the fruiting branches curving inwardly, often with their tips pointing towards terminal antheridia. *Vaucheria racemosa* can easily be distinguished by its downcurved, long pegs from fertile branches bearing pendent oogonia (Blum 1972). *Vaucheria racemosa* is in fact more similar to multiple oogonial forms of *V.*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Figures 20–34. Connecticut freshwater *Vaucheria* species. 20–22. *V. geminata*; 23–27. *V. prona*; 28–34. *V. taylorii*. All scale bars = 100 μm.

*prona*, but that species has long fruiting branches while those in *V. racemosa* are distinctly smaller (Blum 1972).

The antheridial pedicels of *Vaucheria taylorii* project at least to the same height as the tops of oogonia (Figures 28, 30), usually exceeding them and at times being significantly higher (Figures 32, 34), one of the characters used to distinguish it from *V. geminata* (Blum 1971). *Vaucheria taylorii* is further noted by its swollen pedicels (Blum 1971), yet this character is variable among and between the various collections we and others have made (Figures 28–34). Still, unlike *V. geminata*, some of the reproductive branches of *V. taylorii* in a population will be significantly swollen centrally where oogonial pegs are formed (Figures 28, 31, 32). Oogonia range from 61–91 × 64–92 μm, and show a trend from larger and distinctly flattened on adaxial surfaces when only two are formed on a reproductive branch (Figure 29), to smaller and ovate to reniform when present in whorls of three to six (Figures 28, 32).

The only other species we have found with more than two oogonia per fertile branch, *Vaucheria prona*, is easily distinguished by its markedly pendent oogonial pegs (Figure 23). Along with *V. compacta*, *V. taylorii* is one of the least prevalent freshwater species in Connecticut, appearing in only 8% of our collections (Figure 53).

**Vaucheria uncinata* Kütz. 1856, p. 21. Figures 35–38, 54.

TYPE LOCALITY: Freiburg, Germany.

NORTHEAST DISTRIBUTION: Maine, N.H., Mass., Conn., N.Y.

REPRESENTATIVE COLLECTIONS: Fairfield Co.—**SNR1**, *CEL*, coll. 25.x.1998, gam. in field; **NB1**, *CEL*, coll. 28.xi.1997, gam. 25.v.1998. Hartford Co.—**BBB2**, *CWS*, coll. 10.xii.1997, gam. 13.i.1998; **BUR1**, *CWS/CEL*, coll. 5.vi.1998, gam. 28.vi.1998; **CM1**, *CEL*, coll. 1.ix.1998, gam. 10.ix.1998; **FS3**, *CWS/CEL*, coll. 5.vi.1998, gam. 28.vi.1998; **GMS2**, *CWS/CEL*, coll. 5.vi.1998, gam. 28.vi.1998; **GRDD1**, *AN*, coll. 22.ii.1998, gam. 28.v.1998; **GSB2**, *CWS/CEL*, coll. 5.vi.1998, gam. 28.vi.1998; **RGB2**, *CWS/CEL*, coll. 5.vi.1998, gam. 28.vi.1998; **SCR1**, *CEL/CWS*, coll. 5.vi.1998, gam. 14.vi.1998. Litchfield Co.—**PTB1**, *CEL*, coll. 1.ix.1998, gam. 1.x.1998. Middlesex Co.—**SR2**, *CWS*, coll. 28.ix.1997, gam. 11.x.1997. New London Co.—**AR1**, *CEL*, coll. 23.v.1998, gam. 7.vii.1998; **CCR1**, *CEL*, coll. 23.v.1998, gam. 28.vi.1998; **HVP1**, *CEL*, coll. 23.v.1998, gam. 7.vii.1998; **LBM1**, *CWS*, coll. 29.xi.1997, gam. 24.vi.1998; **ST1**, *CEL*, coll. 23.v.1998, gam. 17.vii.1998; **TR1**, *AN/CEL*, coll. 22.x.1997, gam. 28.x.1997. Tolland Co.—**CB1**, *CEL*, coll. 11.ix.1997, gam. 3.ii.1998; **RRB1**, *CEL*, coll.

6.ix.1997, gam. 22.iv.1998. Windham Co.—**NK1**, *AN/CWS*, coll. 18.ix.1997, gam. 30.ix.1997; **NK7**, *MED/CWS*, coll. 29.ix.1998, gam. in field.

REMARKS. The complicated taxonomic and nomenclatural history of this species is summarized by Blum (1953). Our collections represent the first record of *Vaucheria uncinata* for Connecticut, although Blum (1972) reported its distribution throughout the continental United States. It is a somewhat common species in our collections, found in 15% of all sites sampled, occurring almost exclusively in the Connecticut River Valley or to the east of the Connecticut River (Figure 54). We rarely found *V. uncinata* on mud saturated with water in the field and it only appeared in our cultures when the crude samples became somewhat dried.

*Vaucheria uncinata* is easily distinguished from the other local species by its unusually large, transversely elongated, pendent oogonia (108–150 μm in greatest dimension) that often appear to be sessile on the siphons due to their terminal position on long, hooked, or gallows-shaped, reproductive branches (Figures 35–38). In certain locations during the fall, we have found fertile *V. uncinata* growing as an extensive mat over mud in non-flowing intermittent streams.

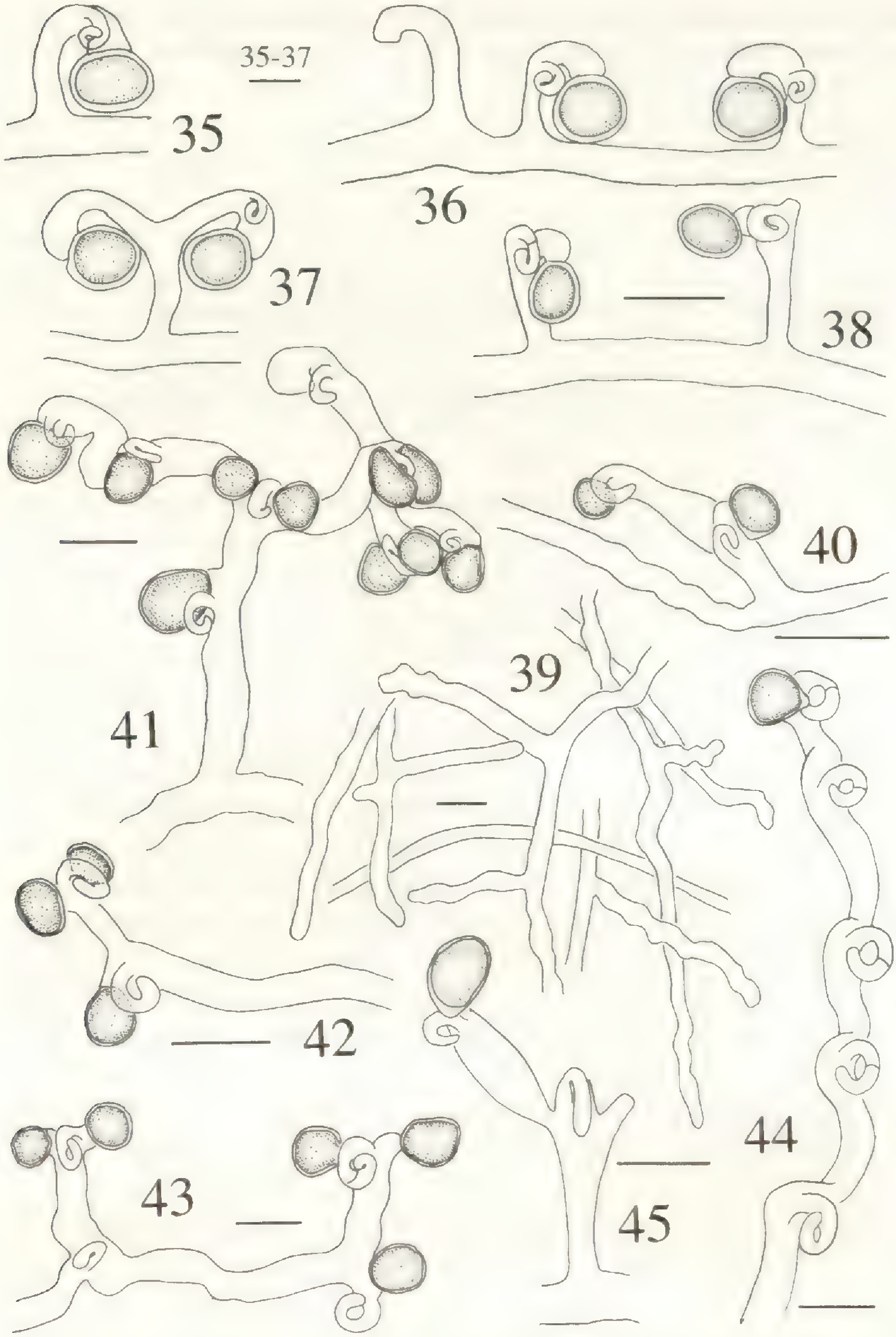
**Vaucheria undulata* C. C. Jao 1936, p. 741.

Figures 39–45, 55

TYPE LOCALITY: Fou-tu-Kuan, Szechwan, China.

NORTHEAST DISTRIBUTION: Maine, Mass., Conn., R.I., N.Y., N.J.

REPRESENTATIVE COLLECTIONS: Fairfield Co.—**AC1**, *CEL*, coll. 30.viii.1998, gam. 18.ix.1998; **BSP1**, *CEL*, coll. 31.v.1998, gam. 6.vi.1998; **CD1**, *CEL*, coll. 31.v.1998, gam. 14.vi.1998; **CPG1**, *CEL*, coll. 31.v.1998, gam. 6.vi.1998; **KP1**, *CEL*, coll. 25.x.1998, gam. in field; **NB1**, *CEL*, coll. 28.xi.1997, gam. 28.v.1998; **NCM1**, *CEL*, coll. 25.x.1998, gam. 12.xi.1998; **PB1**, *CEL*, coll. 28.xi.1997, gam. 17.vii.1998; **PN1**, *CEL*, coll. 31.v.1998, gam. 6.vi.1998; **SNR1**, *CEL*, coll. 25.x.1998, gam. in field. Hartford Co.—**BRWB**, *CWS*, coll. 12.xii.1997, gam. 23.v.1998; **CP1**, *AN*, coll. 22.ii.1998, gam. 3.ix.1998; **FMT1**, *CEL*, coll. 25.x.1998, gam. 12.xi.1998; **FWB1**, *CEL/CWS*, coll. 5.vi.1998, gam. 6.x.1998; **GMS1**, *CEL/CWS*, coll. 5.vi.1998, gam. 28.vi.1998; **GRDD1**, *AN*, coll. 22.ii.1998, gam. 30.v.1998; **MP1**, *CEL*, coll. 8.x.1997, gam. 15.x.1997; **RGB2**, *CEL/CWS*, coll. 5.vi.1998, gam. 14.vi.1998; **SBBB1**, *CEL*, coll. 21.x.1997, gam. 29.xi.1997; **SCR1**, *CEL/CWS*, coll. 5.vi.1998, gam. 14.vi.1998; **WCP1**, *AN*, coll. 22.ii.1998, gam. 28.v.1998. Litchfield Co.—**EA1**, *CEL*, coll. 1.ix.1998, gam. 21.ix.1998; **KFB1**, *CEL*, coll. 30.vii.1998, gam. 12.xi.1998; **PR2**, *CEL*, coll. 1.ix.1998, gam. in field; **PTB1**, *CEL*, coll. 1.ix.1998, gam. 23.ix.1998. Middlesex Co.—**SR2**, *CWS*, coll. 28.ix.1997, gam. 23.xii.1997. New Haven Co.—**DL1**, *CEL/*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Figures 35–45. Connecticut freshwater *Vaucheria* species. 35–38. *V. uncinata*; 39–45. *V. undulata*. All scale bars = 100 μm.

*AN*, coll. 3.xii.1997, gam. 3.ii.1998; **HB1**, *CEL/AN*, coll. 3.xi.1997, gam. 30.v.1998; **TSB1**, *CEL*, coll. 1.xi.1998, gam. 23.ix.1998; **WBSP1**, *CEL*, coll. 31.v.1998, gam. 9.ii.1999. New London Co.—**AR1**, *CEL*, coll. 23.v.1998, gam. 10.x.1998; **CCR1**, *CEL*, coll. 23.v.1998, gam. 6.vi.1998; **HVP1**, *CEL*, coll. 23.v.1998, gam. 17.vii.1998; **LBM1**, *CWS*, coll. 29.xi.1997, gam. 24.vi.1998; **TAB1**, *CEL*, coll. 23.v.1998, gam. 17.vii.1998; **TR1**, *CEL/AN*, coll. 22.x.1997, gam. 4.xii.1997. Tolland Co.—**CLB1**, *CEL*, coll. 20.viii.1998, gam. 24.x.1998; **MNE1**, *CWS*, coll. 12.iii.1998, gam. 6.vi.1998; **RRB1**, *CEL*, coll. 6.xi.1997, gam. 20.v.1998; **TD1**, *CWS*, coll. 5.x.1997, gam. 10.x.1997; **US1**, *CWS*, coll. 7.xii.1997, gam. 28.v.1998. Windham Co.—**BK1**, *CEL*, coll. 20.viii.1998, gam. 28.i.1999; **LR1**, *CEL*, coll. 20.viii.1998, gam. 12.xi.1998; **NK1**, *AN/CWS*, coll. 18.ix.1997, gam. 16.vi.1998; **NK7**, *MED/CWS*, coll. 29.ix.1998, gam. in field; **QR1**, *CEL*, coll. 20.viii.1998, gam. 10.ix.1998.

REMARKS. Since its description from Szechwan, *Vaucheria undulata*, with its trademark spiraled siphons, has been found in many New England locations (Blum 1972; Colt 1985), and here we add it to the flora of Connecticut. We have found this species to be widespread throughout the state (Figure 55), and it was the most prevalent species in our crude cultures (39%). In the past, *V. undulata* was undoubtedly misidentified as other species, collectors not recognizing it by the majority of siphons that develop spirally at the tips (Figure 39). However, if gametangia are found on a siphon lacking spiraled development, they could easily be confused with *V. frigida* or *V. prona*, due to similar gametangial morphology and position. All three species have pendent oogonia that are borne on fruiting branches distal to single circinate antheridia, *V. undulata* and *V. frigida* mostly with one oogonium per fruiting branch, *V. prona* usually with two. Unlike the others, *V. undulata* oospores often turn light brown prior to release from the mother siphon. Occasionally, *V. taylorii* produces a few undulating (spiraled?) siphons in a population, but the reproductive branches of the two species are distinct.

In his collections of *Vaucheria undulata* from Maine, Colt (1985) found that vegetative siphons were dimorphic, of either small (7–30 μm diam.) or large size (48–60 μm diam.), with few in the intermediate range. Furthermore, he noted that the smaller diameter axes were usually spiraled, while those of greater diameter were mostly undulate to subundulate. In our cultures, the filaments were found to be of a similar dimorphic range, with approximately 60% showing spiral development in both size classes. Our small-diameter siphons were distinctly spiraled, while the larger ones (mature?) were more swollen and appeared to be undulate. Furthermore, only the larger-sized siphons in our cultures produced gametangia. Oogonia in Connecticut populations ranged from 50–80 × 60–100 μm. The reproductive branches inevitably proliferated at maturity, a phenomenon seen only occasionally in other species such as *V. frigida, V. prona*, and *V. geminata* (Figure 20), but never to the extent of *V. undulata*. New reproductive branches were produced at the site where an opposite oogonium would have formed on the previous pedicel in the same system (Figures 40, 41, 43), often repeating this development sequentially (Figures 42, 44). In our crude cultures, *V. undulata* often grew to the exclusion of other *Vaucheria* species, the latter only appearing after the bloom of *V. undulata* had passed (5–6 weeks).

### KEY TO THE FRESHWATER SPECIES OF *VAUCHERIA* IN CONNECTICUT

1. Antheridia and oogonia on separate plants (dioecious) .... 2
1. Antheridia and oogonia on the same plants (monoecious) ... 3
    2. Antheridia with 1 terminal and mostly 2 lateral discharge pores (Figures 9–11) .... *V. compacta* var. *compacta*
    2. Antheridia with 1 terminal and 1 or 0 lateral discharge pores (Figures 12, 13) ...... *V. compacta* var. *dulcis*
3. Oogonia and antheridia sessile or short-stalked on siphons, not borne on special bisexual fruiting branches (pedicels) ... 4
3. Oogonia and antheridia borne on special bisexual fruiting branches ........................................ 5
    4. Oogonia formed singly or in pairs with long, circinate antheridia between them; oospores completely filling oogonial cavities at maturity; oogonial beaks oriented toward the antheridia, either parallel with the siphons or erect at oblique angles (Figures 4–8) ..... *V. bursata*
    4. Oogonia formed singly, never paired around a single antheridium, usually with small, cylindrical antheridia on both sides; oospores with obvious distal and peripheral oogonial cavities at maturity; oogonia with deflected beaks directed towards the siphons (Figures 1–3) .... ........................................ *V. aversa*
5. Oogonia formed singly on fruiting branches ............ 6
5. Oogonia usually 2 or more on each fruiting branch ...... 7
    6. Oogonia subspherical to transversely elongate, lacking

beaks, pendent on hooked or gallows-shaped pedicels (Figures 35–38) ...................... *V. uncinata*

6. Oogonia subspherical to obovate and reniform with small distal beaks, borne terminally on curved pedicels (Figures 14–19) .......................... *V. frigida*

7. Population rarely containing spiraled siphons; oogonia almost always 2 per fruiting branch (occasionally 1 or 3–4, but these oogonia pendent), borne laterally to terminal erect antheridia; if proliferating additional fruiting branches, usually 2 oogonia maintained on the basal fruiting branch (Figure 20) ................................. 8

7. Population often containing spiraled siphons; oogonia highly variable in number per fruiting branch; if proliferating additional fruiting branches, usually 1 oogonium maintained on the basal fruiting branch (Figures 40–42) ......... 9

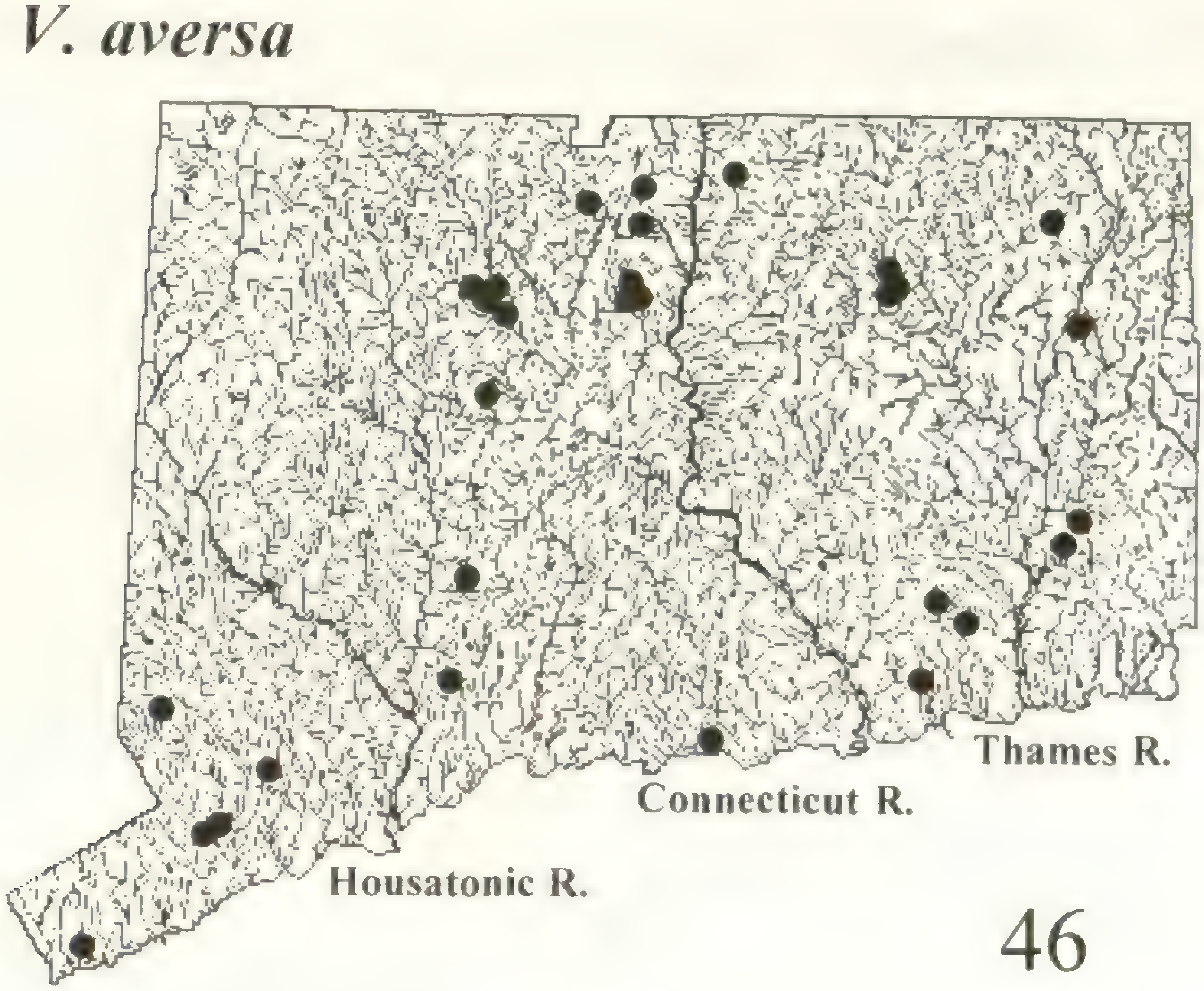
8. Oogonia pendent on obvious downcurved pegs, occasionally numbering 3–4 (Figure 23); fruiting branches usually curved (Figures 24–27) ............. *V. prona*

8. Oogonia erect on pegs and directed away from siphons, almost uniformly numbering 2; fruiting branches straight and erect (Figures 20–22) ..... *V. geminata*

9. Siphons commonly spiralling, especially the thinner ones in a population (Figure 39); oogonia 1 or 2 per fruiting branch, with variation common on individual siphons; fruiting branches commonly proliferating in chain-like fashion from one another at maturity (Figures 40–44); fruiting branches not swollen at points of oogonial attachment at maturity (Figures 41, 42) ............... *V. undulata*

9. Siphons only occasionally spiralling; 2 to 6 oogonia per fruiting branch, with great variation common on individual siphons; fruiting branches distinctly swollen at points of oogonial attachment at maturity (Figures 28–34) ... ......................................... *V. taylorii*

ACKNOWLEDGMENTS. We thank Courtney Hadly, Megan Dunphy, Megan Garretson, and Ginny Schneider for their assistance on this project both in the field and in the lab. We acknowledge a Trinity College student research grant from the Faculty Research Committee to CEL. We appreciate the constructive criticism of the manuscript provided by Dr. Arthur Mathieson (UNH).


V. aversa
Thames R.
Connecticut R.
Housatonic R.

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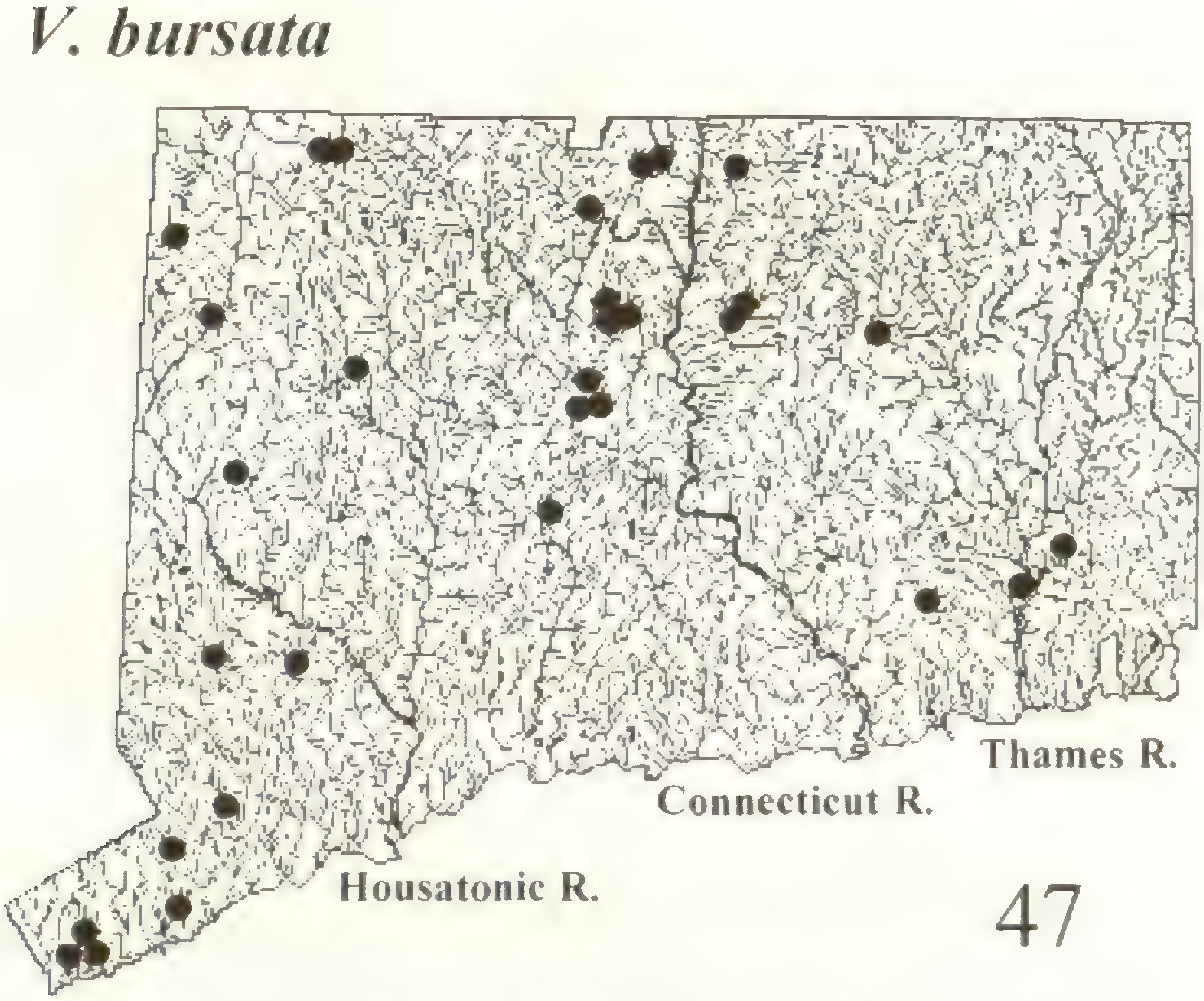
V. bursata
Thames R.
Connecticut R.
Housatonic R.

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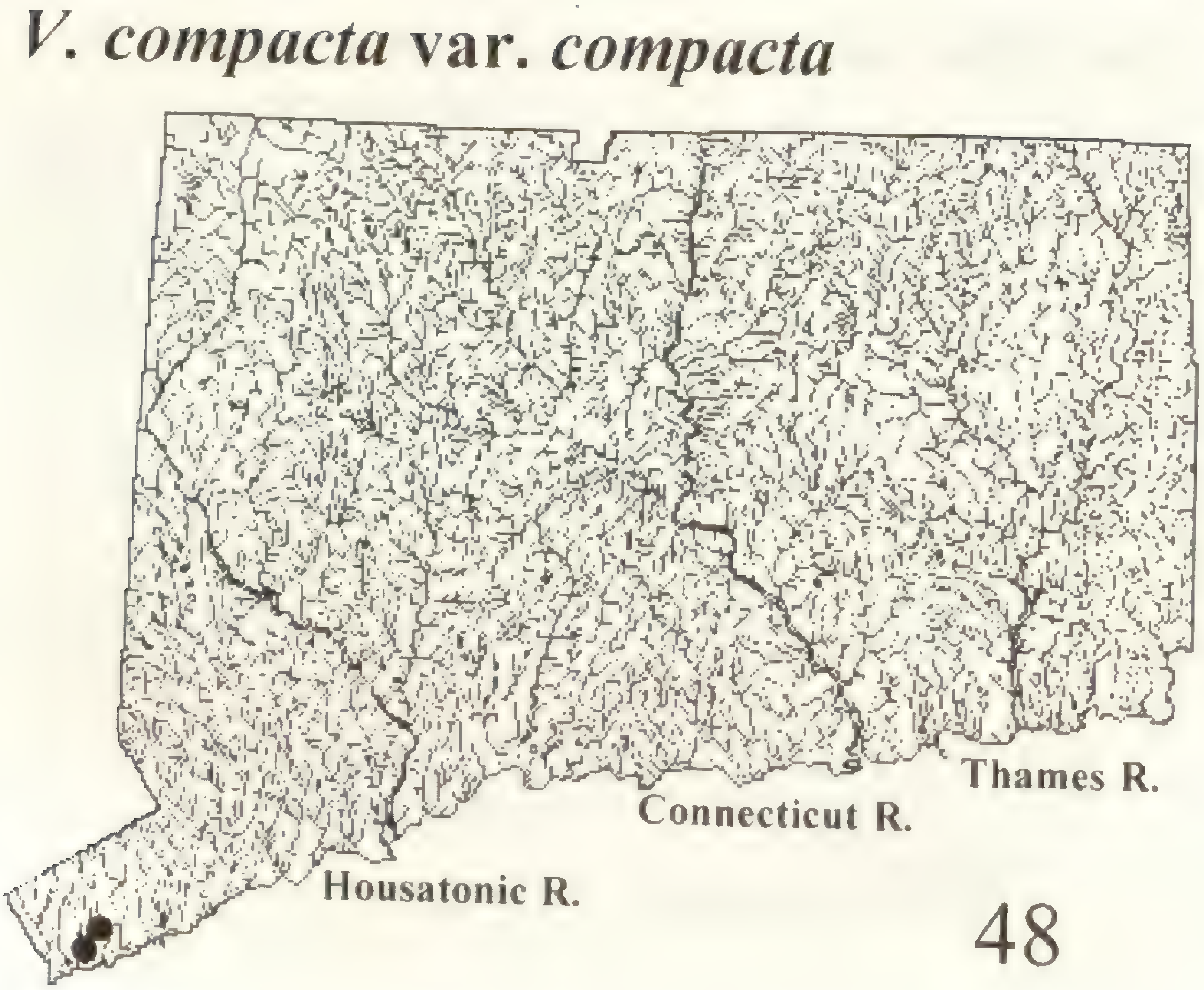
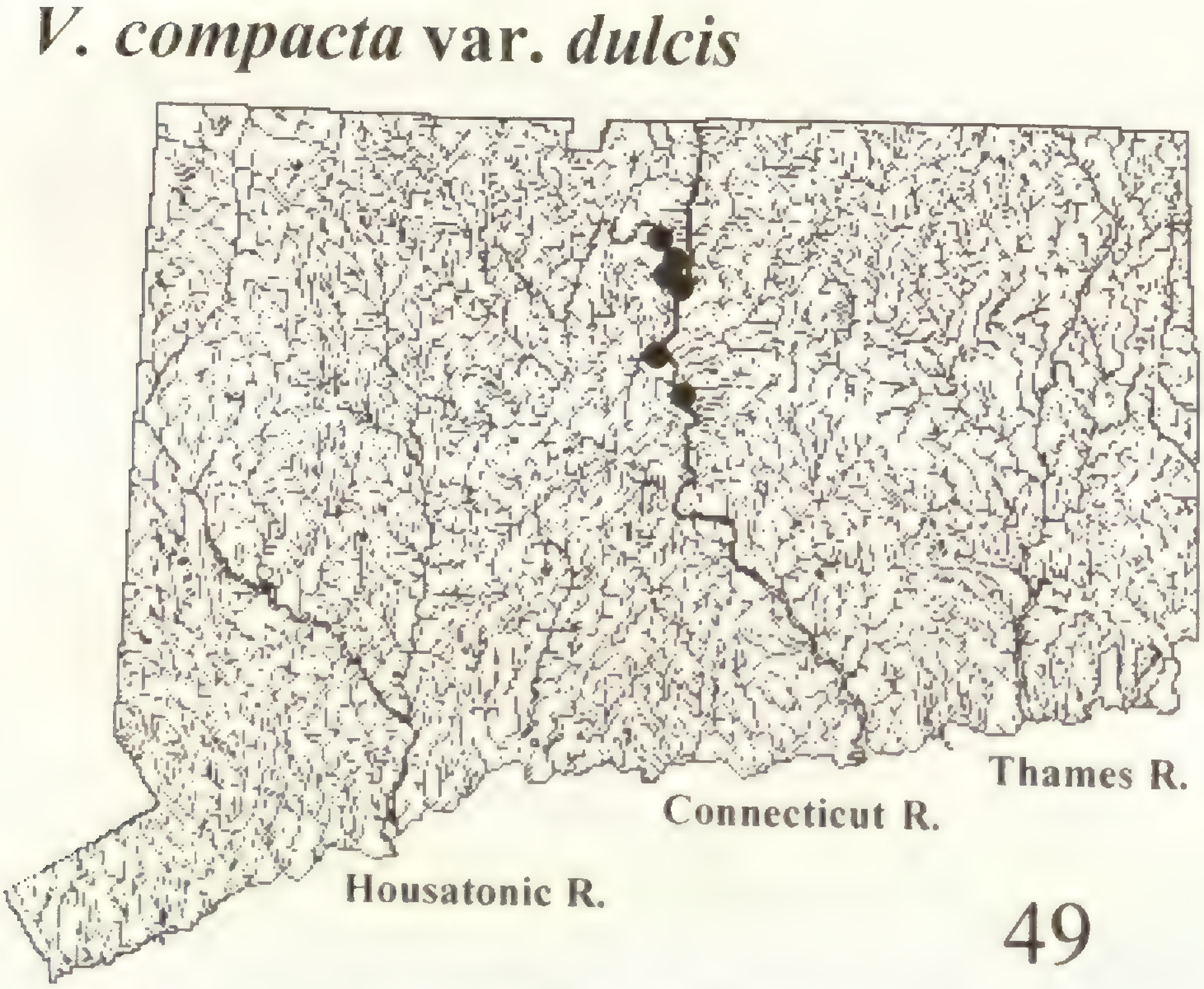
Figures 46–47. Distribution maps of Connecticut freshwater *Vaucheria* species.



*V. compacta* var. *compacta*

Thames R.
Connecticut R.
Housatonic R.

48

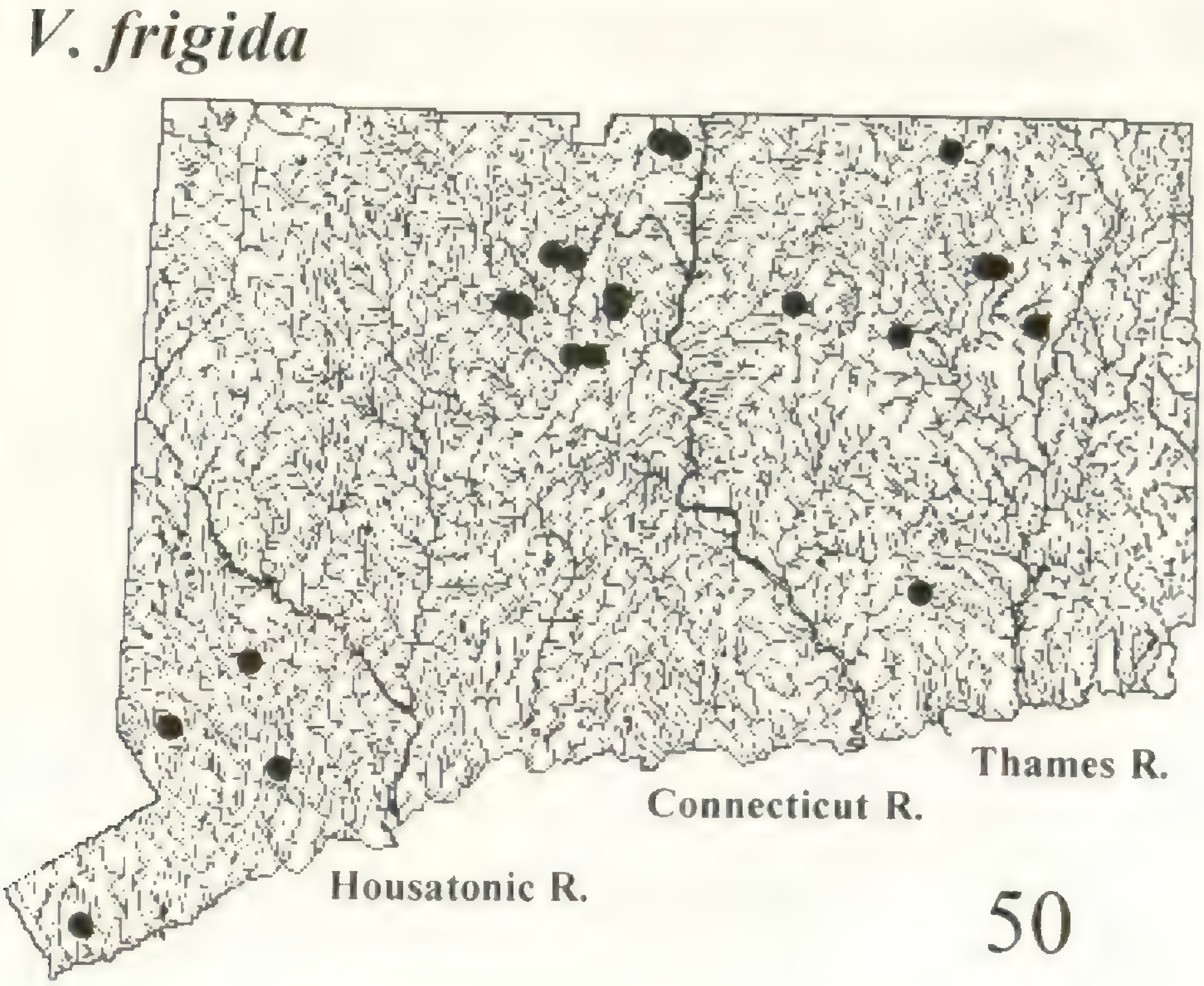


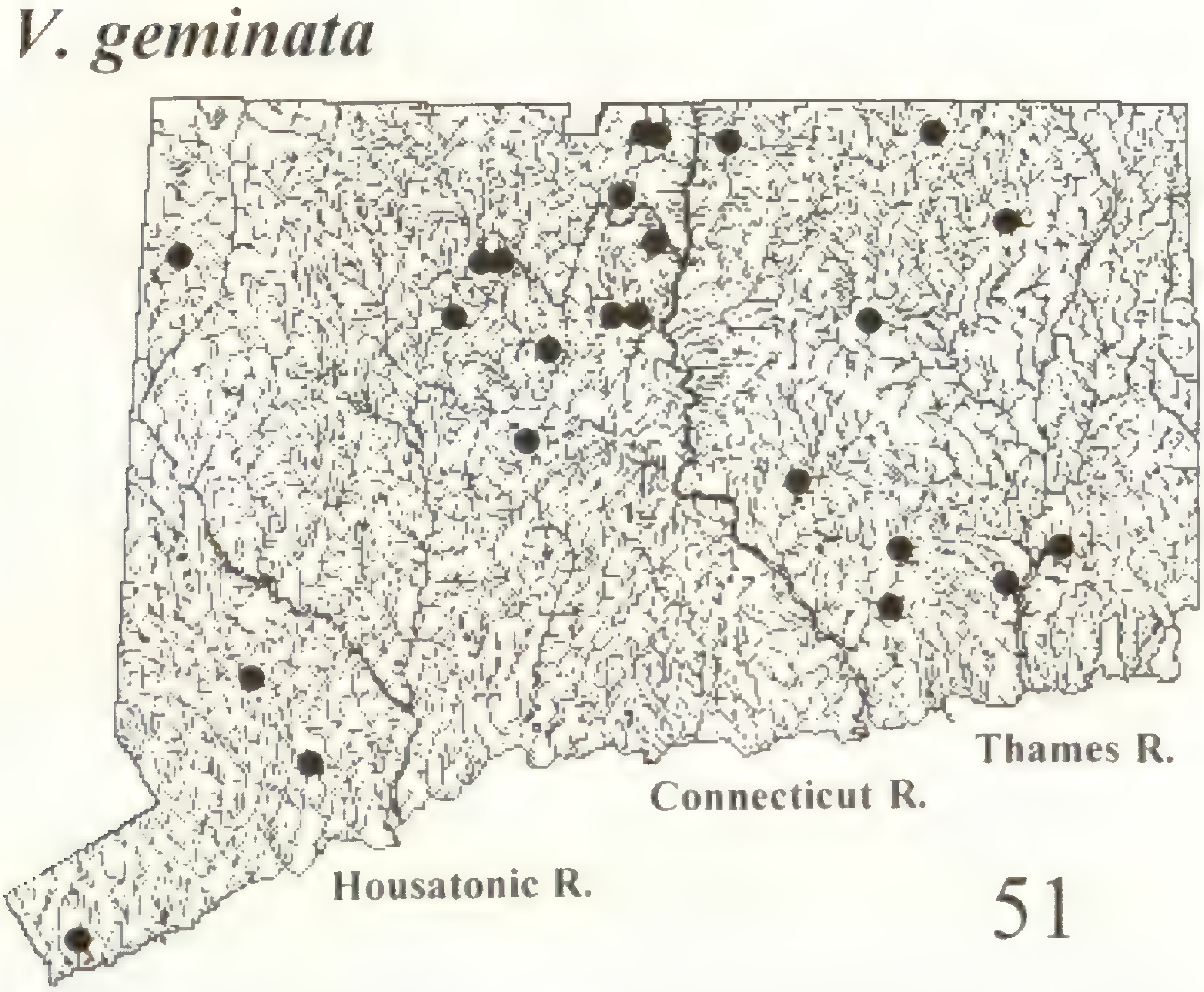
*V. compacta* var. *dulcis*

Thames R.
Connecticut R.
Housatonic R.

49

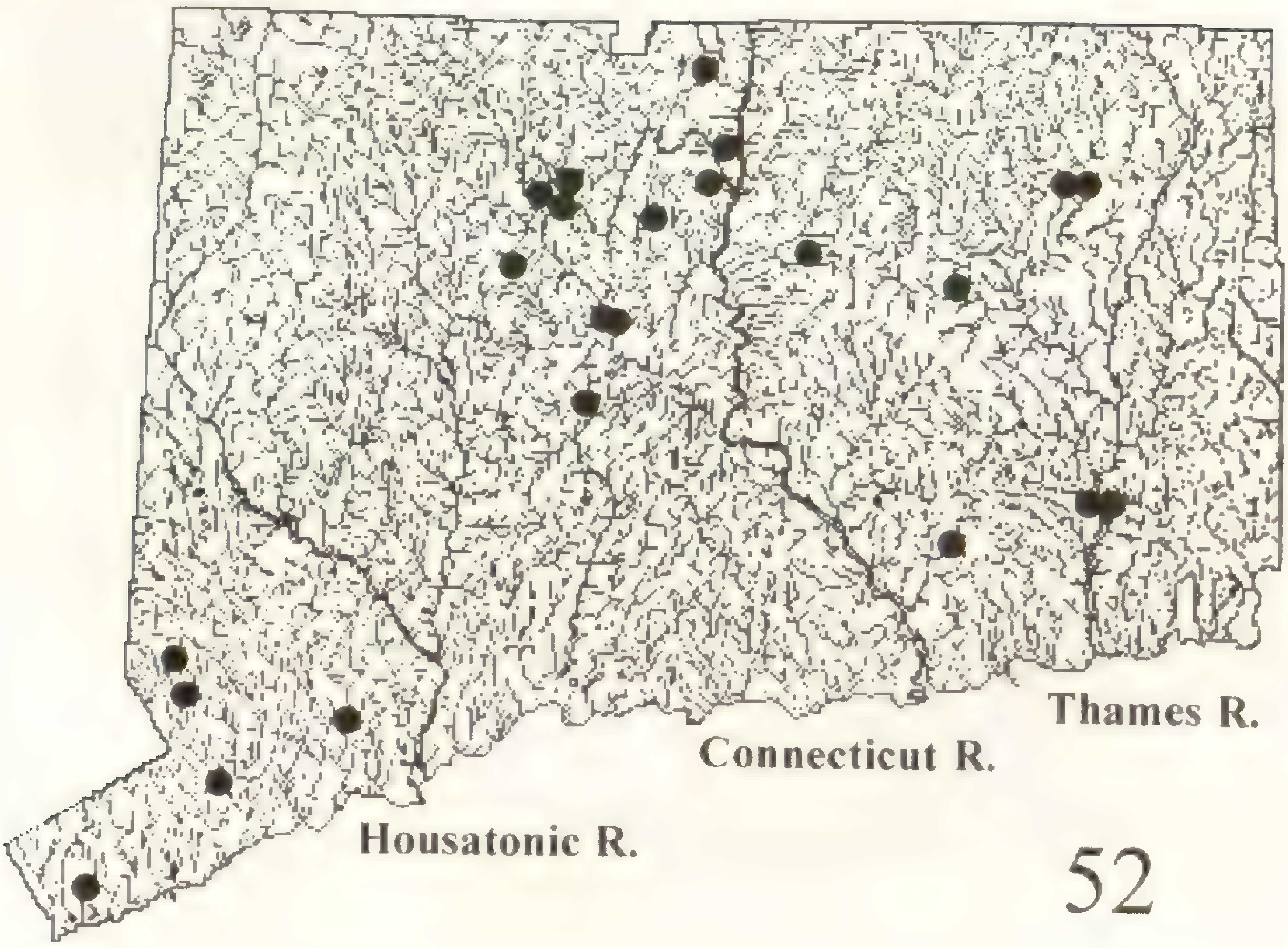
Figures 48–49. Distribution maps of Connecticut freshwater *Vaucheria* species.


*V. frigida*
Thames R.
Connecticut R.
Housatonic R.
50


*V. geminata*
Thames R.
Connecticut R.
Housatonic R.
51

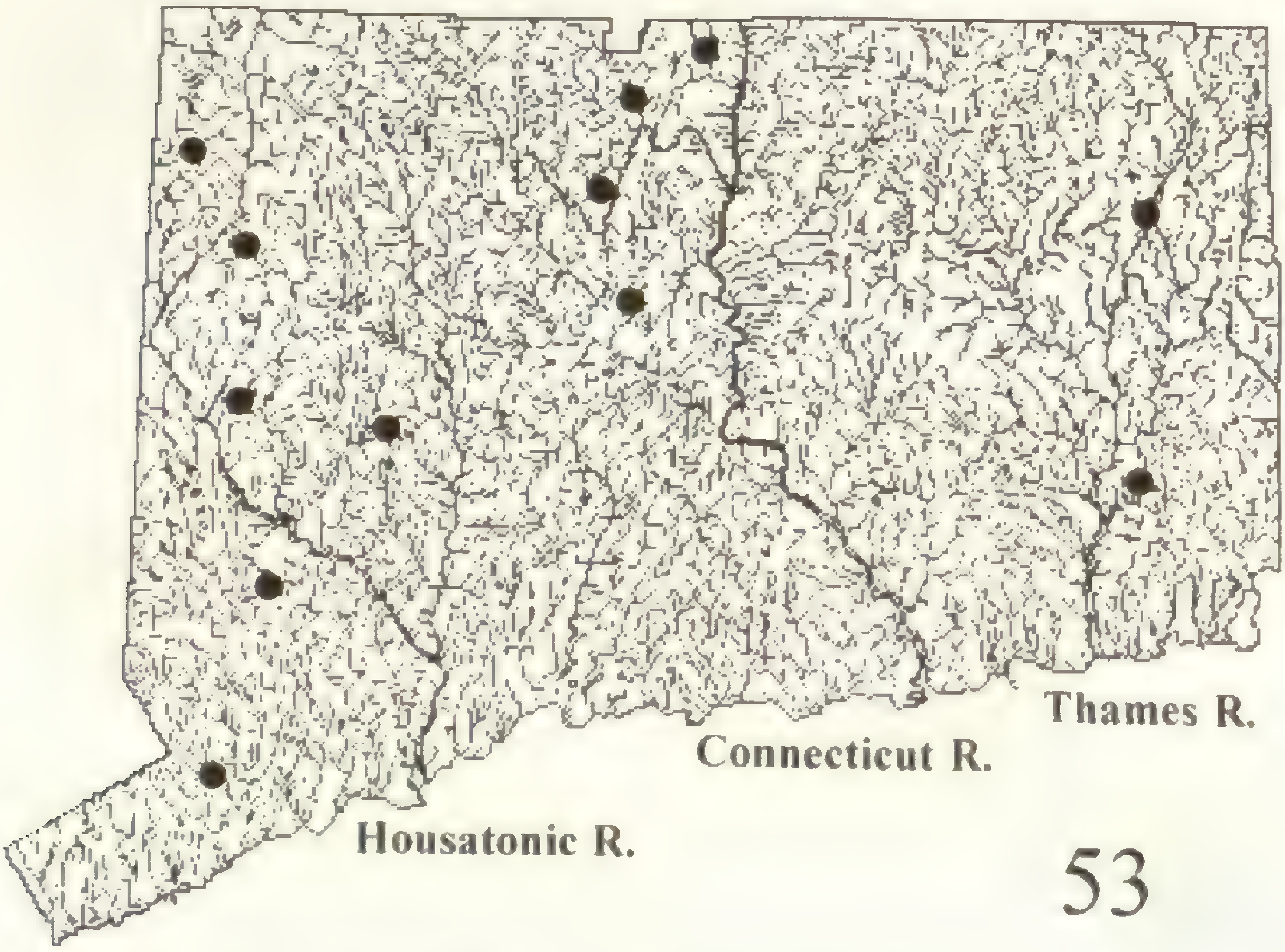
Figures 50–51. Distribution maps of Connecticut freshwater *Vaucheria* species.

*V. prona*


Thames R.
Connecticut R.
Housatonic R.

52

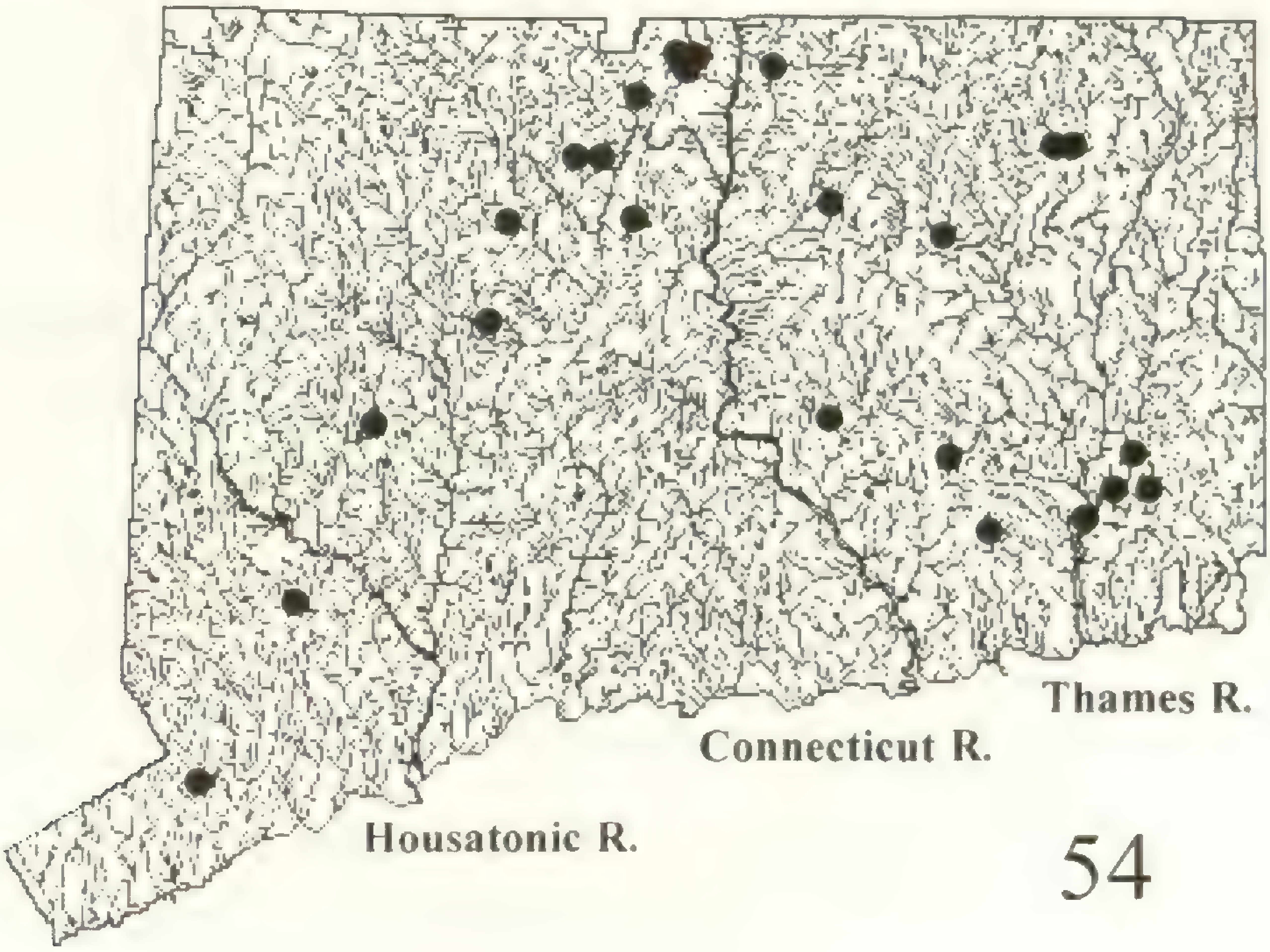
*V. taylorii*


Thames R.
Connecticut R.
Housatonic R.

53

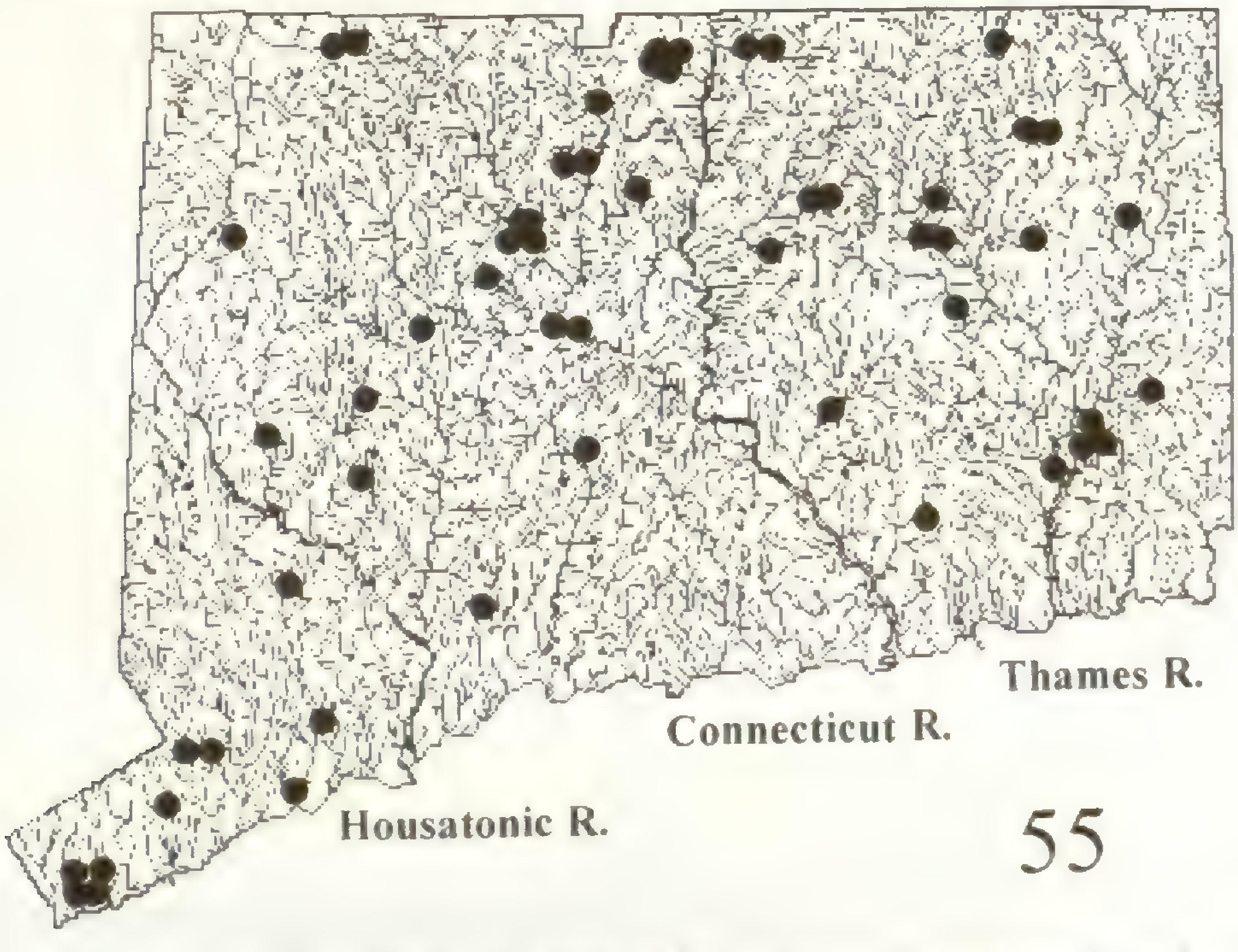
Figures 52–53. Distribution maps of Connecticut freshwater *Vaucheria* species.

***V. uncinata***


Thames R.
Connecticut R.
Housatonic R.

54

***V. undulata***


Thames R.
Connecticut R.
Housatonic R.

55

Figures 54–55. Distribution maps of Connecticut freshwater *Vaucheria* species.

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## APPENDIX

### FRESHWATER COLLECTION SITE CODES.

**AB** — Tolland Co.: Ash Brook, Coventry.
**AC** — Fairfield Co.: Ash Creek, Bridgeport.

**AR** — New London Co.: Blissville Brook, Lisbon.
**BBB** — Hartford Co.: Beamans Brook, Bloomfield.
**BBR** — Litchfield Co.: Blackberry River, North Caanan.
**BBS** — New London Co.: Big Brook, Salem.
**BK** — Windham Co.: Blackwell Brook, Brooklyn.
**BNB** — Litchfield Co.: Butternut Brook, Litchfield.
**BPG** — Fairfield Co.: Bruce Park, Greenwich.
**BRWB** — Hartford Co.: Tunxis Floodwater Retention Reservoir, Wash Brook, Bloomfield.
**BSP** — Fairfield Co.: Bible Street Park, Greenwich.
**BUR** — Hartford Co.: Burlessons Brook, Suffield.
**CB** — Tolland Co.: Brook off Route 44, Coventry.
**CCR** — New London Co.: Cato Corner Road, Colchester.
**CD** — Fairfield Co.: Carrington Drive roadside ditch, Greenwich.
**CLB** — Tolland Co.: Columbia Lake Brook, Columbia.
**CM** — Hartford Co.: Copper Mine Brook, Bristol.
**CP** — Hartford Co.: Covilli's Pond, Canton.
**CPG** — Fairfield Co.: Capalbo Place, Greenwich.
**DL** — New Haven Co.: Lake Dawson, Woodbridge.
**DLF** — New Haven Co.: Cow Pen Hill Road, Madison.
**EA** — Litchfield Co.: East Aspetuck River, New Milford.
**EGST** — Hartford Co.: Tributary Salmon Brook, East Granby.
**EMR** — New Haven Co.: East Mountain Reservoir, Prospect.
**FMT** — Hartford Co.: Farmington River, Tariffville mill, Simsbury.
**FP** — Hartford Co.: Farmington River, Poquonic/Windsor.
**FS** — Hartford Co.: Farmington River, Simsbury.
**FTS** — Hartford Co.: Farmington River, Curtiss Fields, Tariffville/Simsbury.
**FW** — Hartford Co.: Farmington River, Windsor.
**FWB** — Hartford Co.: Freshwater Brook, Enfield.
**GMS** — Hartford Co.: Mountain Brook, Great Marsh, Suffield.
**GRDD** — Hartford Co.: Gracey Road drainage ditch, Canton.
**GSB** — Hartford Co.: Salmon Brook, Granby.
**HB** — New Haven Co.: Junction Route 5 and Interstate 691, Meriden.
**HLM** — Hartford Co.: Hockanum River, Laurel Marsh, Manchester.
**HOR** — Litchfield Co.: Housatonic River, Sharon.
**JB** — Hartford Co.: Jim Brook, Canton.
**KFB** — Litchfield Co.: Kent Falls Brook, North Kent.
**KP** — Fairfield Co.: Kent Pond, Wilton.
**LBM** — New London Co.: Latimer Brook, Montville.
**LEL** — New London Co.: Latimer Brook, East Lyme.
**LJB** — Hartford Co.: Lower Jim Brook, Canton.
**LR** — Windham Co.: Little River, Hampton.
**LV** — Hartford Co.: Farmington River, Farmington.
**MB** — Fairfield Co.: Miry Brook, Danbury.
**MNE** — Tolland Co.: Junction Eaglesville Road/Hunting Lodge Road, Storrs/Mansfield.
**MP** — Hartford Co.: Drainage catchment basin (pond), Interstate-84, Manchester.

**NB** — Fairfield Co.: North Brook, Newtown.
**NBBB** — Hartford Co.: North Branch Bunnel Brook, Burlington.
**NCM** — Fairfield Co.: Mill Pond, New Caanan.
**NCWR** — Litchfield Co.: Witing River, North Caanan.
**NH** — Hartford Co.: Drainage ditch, Route 30, South Windsor.
**NK** — Windham Co.: Nipmuck Trail, Ashford.
**NN** — Litchfield Co.: Nonnewaug River, Woodbury.
**NR** — Fairfield Co.: Norwalk River, Ridgefield.
**NRS** — Hartford Co.: Floodplain vic. Wells Pond, West Hartford.
**PB** — Fairfield Co.: Patterson Brook, Easton.
**PBW** — Hartford Co.: Phelps Brook, Windsor.
**PGB** — Hartford Co.: Plum Gully Brook, South Windsor.
**PN** — Fairfield Co.: Montgomery Pinetum, Greenwich.
**PR** — Litchfield Co.: Pequabuck River, Plymouth.
**PTB** — Litchfield Co.: Purgatory Brook, Watertown.
**QP** — Hartford Co.: Quinnipiac River, Southington.
**QR** — Windham Co.: Quinebaug River, Brooklyn.
**RGB** — Hartford Co.: Rocky Gutter Brook, Suffield.
**RP** — Hartford Co.: Reservoir pond, West Hartford.
**RPC** — Hartford Co.: Riverside Park, Connecticut River, Hartford.
**RRB** — Tolland Co.: Valley Falls Park, Vernon.
**RRD** — New London Co.: Drainage ditch, Roosevelt Road, Norwich.
**SBBB** — Hartford Co.: South Branch Bunnel Brook, Burlington.
**SCR** — Hartford Co.: Scantic River, Enfield.
**SDD** — New London Co.: Route 11 drainage pond, junction Route 82, Salem.
**SKR** — Tolland Co.: Skungamaug River, Coventry.
**SNR** — Fairfield Co.: South Norwalk Reservoir, Wilton.
**SR** — Middlesex Co.: Salmon River, East Hampton.
**ST** — New London Co.: Shetucket River, Taftville.
**TAB** — New London Co.: Taftville area brook, Lisbon.
**TD** — Tolland Co.: Taylor Road, railroad cut drainage ditch, Vernon.
**TMR** — Hartford Co.: Lazy Lane Road, Southington.
**TR** — New London Co.: Shetucket River, Norwich.
**TSB** — New Haven Co.: Transylvania Brook, Southbury.
**US** — Tolland Co.: Stream, Route 171, Union.
**WBB** — Hartford Co.: Wash Brook, Bloomfield.
**WBSP** — New Haven Co.: Wharton Brook State Park, outlet brook, Wallingford.
**WCP** — Hartford Co.: Woodridge Circle Pond, Canton.
**WHR** — Hartford Co.: West Hartford Reservoir, West Hartford.
**WMR** — Fairfield Co.: Stream, Wire Mill Road, Stamford.
**WP** — Hartford Co.: Wells Pond, West Hartford.
**WPF** — Hartford Co.: Wells Pond feeder stream, West Hartford.

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# DISTURBANCE AS A FACTOR IN THE DISTRIBUTION OF SUGAR MAPLE AND THE INVASION OF NORWAY MAPLE INTO A MODIFIED WOODLAND

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ABSTRACT. Disturbances have the potential to increase the success of biological invasions. Norway maple (*Acer platanoides*), a common street tree native to Europe, is a foreign invasive with greater tolerance and more efficient resource utilization than the native sugar maple (*Acer saccharum*). This study examined the role disturbances from a road and path played in the invasion of Norway maple and in the distribution of sugar maple. Disturbed areas on the path and nearby undisturbed areas were surveyed for both species along transects running perpendicular to a road. Norway maples were present in greater number closer to the road and on the path, while the number of sugar maples was not significantly associated with either the road or the path. These results suggest that human-caused disturbances have a role in facilitating the establishment of an invasive species.

Key Words: invasive plants, Norway maple, *Acer platanoides*, sugar maple, *Acer saccharum*, disturbance

Biological invasions happen when non-native species are introduced into new environments (Drake 1988). Although many of these species are absorbed into the community without influencing it very much (Begon et al. 1996), the detrimental effects of some invasives have been recognized as one of the major threats to biological diversity (Soule and Kohm 1989). These species may alter population dynamics, community structure (Elton 1958; Mooney and Drake 1986), and ecosystem structure and diversity (Vitousek 1990).

While natural disturbances often increase species richness and diversity (Hobbs and Hunneke 1992), they can also increase the likelihood of invasion. The potential for invasion is enhanced when a combination of disturbances is present (Hobbs 1991). For this study, disturbance refers to events that stress the community and influence resource availability and mortality rates. Examples include soil exposure, edge effects, nutrient addition (Hobbs 1991), and any event that removes plants, leaving a space open for colonization (Begon et al. 1996).

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One common type of disturbance occurs when an edge of a community faces a more open area, such as a field, path, road, or body of water. An "edge effect" occurs because the edges of a forest have a different microclimate than the forest interior. This results in a different plant species composition, including a higher number of exotics, and different community structure. In North Carolina, Fraver (1994) measured the percent cover of individual species and the relative cover of exotic species, and found edge effects extended 20–60 m into the interior of the forest. In addition, exotics were found mainly on the edges and did not make up a significant portion of the forest interior. In Pennsylvania and Delaware, the edge effect significantly influenced light, temperature, litter moisture, humidity, and shrub cover up to 50 m from the edge (Matlack 1993).

A primary reason for the spread and establishment of invasive species is their introduction by humans as crops, ornamentals, or for forestry (Elton 1958). Norway maple (*Acer platanoides* L.) is an ornamental that has been described as an invasive exotic in urban forests in New Jersey (Webb and Kaunzinger 1993), Pennsylvania (Kloeppel and Abrams 1995), and Great Britain (Nowak and Rowntree 1990). Norway maple is the widest ranging maple in its native European habitat. Introduced into the United States in 1756 by John Bartram of Philadelphia, its optimal range in the United States includes coastal northern New England, southern New England, and the Midwest (Nowak and Rowntree 1990). It may be able to transform the native woodland by outcompeting sugar maple (*Acer saccharum* Marshall; Webb and Kaunzinger 1993), which is native to the United States.

Norway maple and sugar maple grow side by side as street trees and in urban forests and share many life-history characteristics. Both species produce seeds in the fall that require 2–3 months of stratification before spring germination (Hartmann et al. 1990) and both have been described as shade tolerant in their native ranges (Diekmann 1996; Sipe and Bazzaz 1995). Sugar maple grows best in small gaps (Runkle 1984). Although it grows faster in a gap than in the closed canopy (Canham 1988), sugar maple has a strong negative correlation with large gaps of $400 m^2$ (Runkle 1984).

Norway maple has certain advantages that allow it to outcompete sugar maple and influence species composition when it invades urban woodlands. Since its introduction, Norway maple has become one of the most widely planted street trees due to its longevity, disease resistance, and ability to withstand poor soils and pollution. In urban areas, its wide tolerances and abundant seeds allow it to colonize woodlots and urban forests (Spongberg 1990). Norway maple also has a physiological advantage over sugar maple due to its higher rate of photosynthesis, longer retention of leaves in the fall, and faster sapling growth (Kloeppel and Abrams 1995). In addition, Norway maple can influence community structure. In a New Jersey sugar maple/beech/oak forest that had been invaded by Norway maple, the understory species richness for each of the canopy trees was compared. Norway maple had a significantly lower species richness in its understory than the other tree species (Wyckoff and Webb 1996).

The purpose of this study was to determine if there is a correlation between disturbance and the establishment of Norway maple.

## STUDY SITE

The Middlesex Fells Reservation in eastern Massachusetts was created in 1894. European colonists, arriving in the area in the 1600s, used the land primarily for farming but also for mills, firewood, cattle grazing, and mining (Levin and Mahlstedt 1990). Today the Fells is a mostly wooded, popular urban retreat. Only 10 km north of Boston, it is located in the towns of Winchester, Stoneham, Melrose, Malden, and Medford. Routes 23 and 93 run through the middle of the Reservation and divide it into eastern and western halves. Two-lane paved roads run along the perimeter, with Norway maples planted as street trees in some areas. The trees range from 10–40 cm in diameter. No record could be found of exactly when they were planted, but all are large enough to produce seeds.

The western side of the Fells, where this study was done, covers about 400 ha. The landscape changes greatly over short distances, due to high ridges with exposed ledges that run north to south with slopes running down to streams, ponds, and large manmade reservoirs (Drayton and Primack 1996). Foot, animal, and mountain bike traffic can be heavy on the extensive 3–5 m wide carriage roads and the smaller footpaths. The first major carriage paths were likely due to the creation of the reservoirs from 1870–1901. Later, in the 1930s, the Civilian Conservation Corps and the Works Progress Administration also built many roads and paths (Levin and Mahlstedt 1990).

## MATERIALS AND METHODS

Twenty-four transects were established perpendicular to the paved roads along the western side of the Middlesex Fells Reservation. At each of twelve sites two parallel transects were set up, one with a path as the transect line (disturbed), and another 20 m away in an area with no path (undisturbed). Along each transect, 10 × 10 m plots were established with the first plot at the road. On the transect that ran along the path, half of each plot was placed on either side of the path. The next two plots leading away from the road (numbers 2 and 3) had 50 m between them, with 100 m between remaining plots (Figure 1). Sampling was discontinued when the plots had no Norway maples, and a visual inspection showed no more further on. In each plot, the number of Norway and sugar maples above 50 cm in height was counted.

To determine the influence of the path, a Mann-Whitney test was performed on the number of Norway maples and sugar maples on and off of the path. To determine the influence of the road, a Mann-Whitney test was performed comparing the number of Norway maples and sugar maples in plots 1 and 2. Plots 2 and 3 were also compared. Only the first three plots at each site, both on and off the path, were used in the analysis due to the lack of replication for plots 4–6. All statistical analysis was done on SPSS (SPSS, Version 6.1, Chicago, Illinois).

## RESULTS

The path and distance from the road (using plot as a proxy for distance) correlated with the presence of Norway maples but not the presence of sugar maples. Results of the Mann-Whitney tests indicated there were significantly more Norway maples closer to the road and on the path (Figure 2; path: $df=65$, $Z=-2.538$, $P=0.011$; plot 1–plot 2: $df=49$, $Z=-3.628$, $P<0.001$; plot 2–plot 3: $df=41$, $Z=-1.345$, $P=0.179$). Results of the Mann-Whitney tests indicated that the number of sugar maples was not affected by the road or path (Figure 3; path: $df=65$, $Z=-0.367$, $P=0.713$; plot 1–plot 2: $df=49$, $Z=-0.504$, $P=0.614$; plot 2–plot 3: $df=41$, $Z=-0.699$, $P=0.484$).

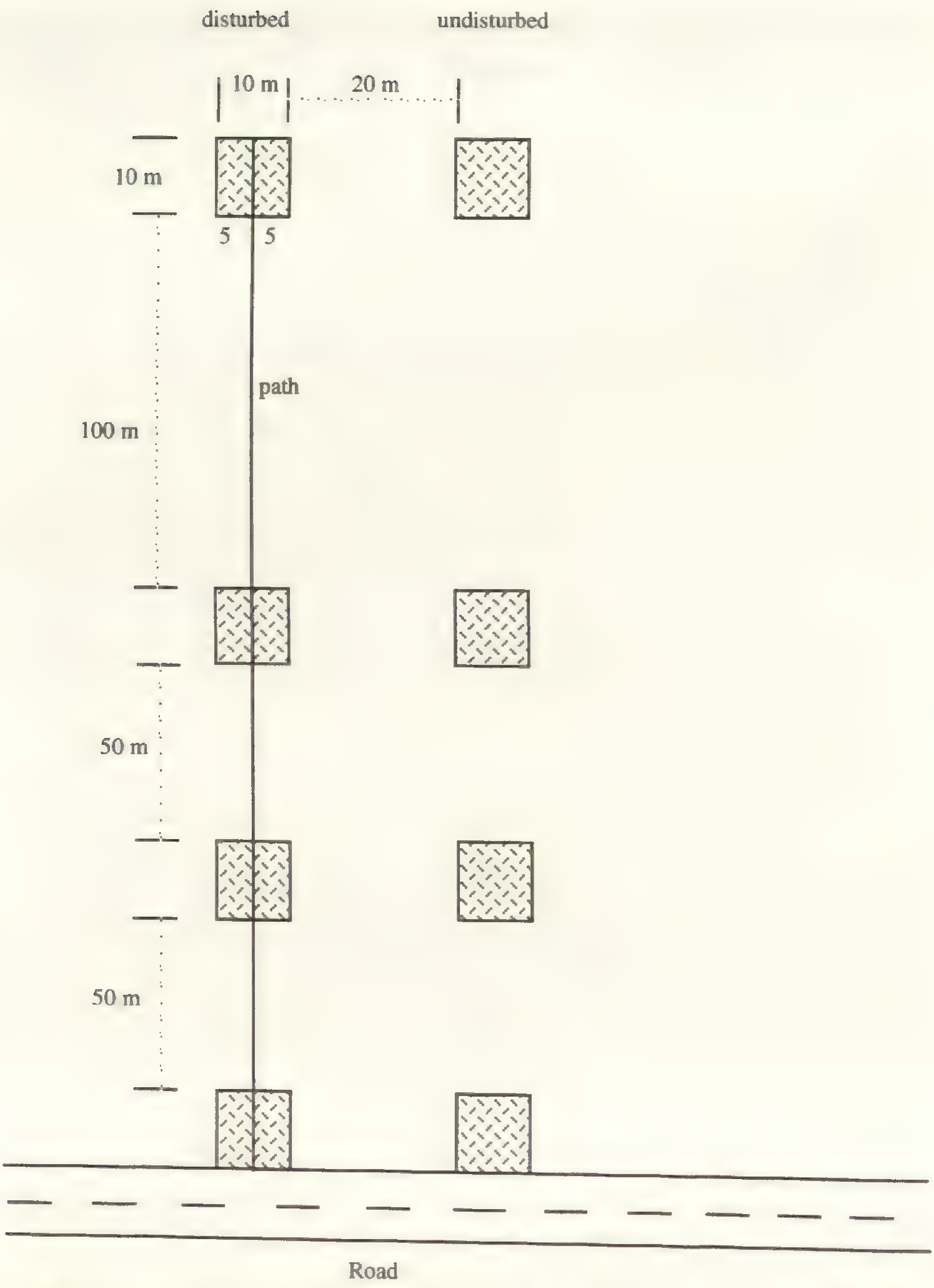
disturbed
undisturbed
10 m
20 m
10 m
5
5
path
100 m
50 m
50 m
Road

Figure 1. Representation of placement of transects and plots at the Middlesex Fells Reservation.

## DISCUSSION

Two specific factors were hypothesized to aid Norway maple's invasion. First, that the road, planted with Norway maples as street trees, created an edge effect and acted as a seed source.

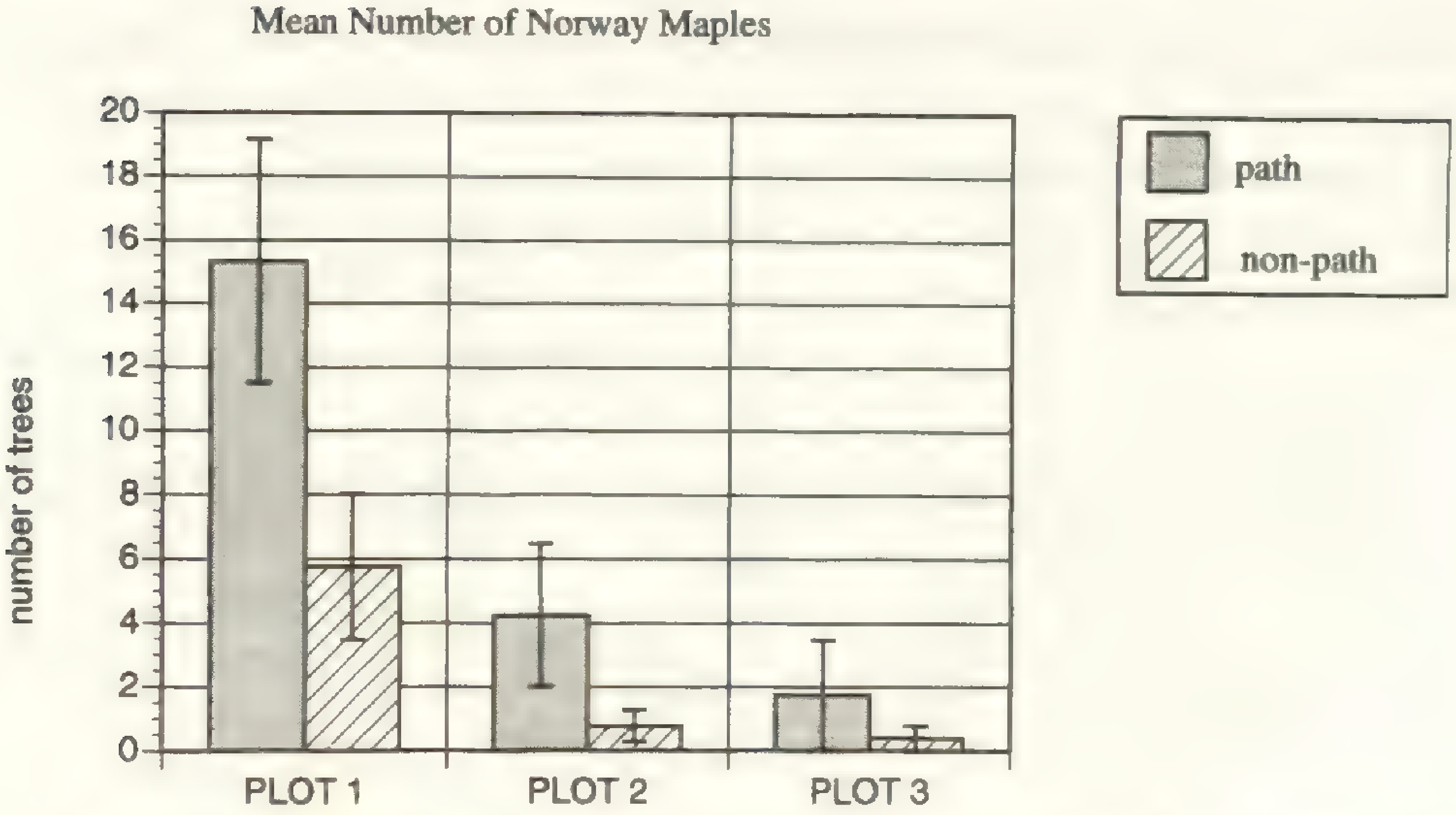

Figure 2. Mean number of Norway maples in plots 1–3 at the Middlesex Fells Reservation. Error bars indicate ±1 SE.

Second, that the paths running perpendicular to the road allowed Norway maple to penetrate greater distances along the path than in nearby nondisturbed areas with no paths.

As hypothesized, there were significantly more Norway maples by the road and on the path (Figure 2). The effect of the road seems not to have exceeded 50 m, as there was no significant difference in the number of Norway maple trees in plots 2 and 3. It is possible that there were more Norway maples closer to the road because there were abundant seeds from the nearby street trees, and not due to Norway maple's tolerance for salt or other edge effects. Even if edge effects were not a significant factor, the path seems to have acted as a place for Norway maple to become established.

Since sugar maple abundance has been shown to have a significant negative correlation with large gaps (Runkle 1984), its abundance was expected to increase with distance from the road. Contrary to expectations, the presence of sugar maples was not significantly affected by the road or the path (Figure 3). The edge effects may not have been strong enough to influence the sugar maple.

These results suggest that Norway maple relies more on disturbed habitats for establishment than sugar maple does. Invasive plants can follow one of two patterns, either advancing in a front or as scattered small populations (Baker 1986). Species that de-

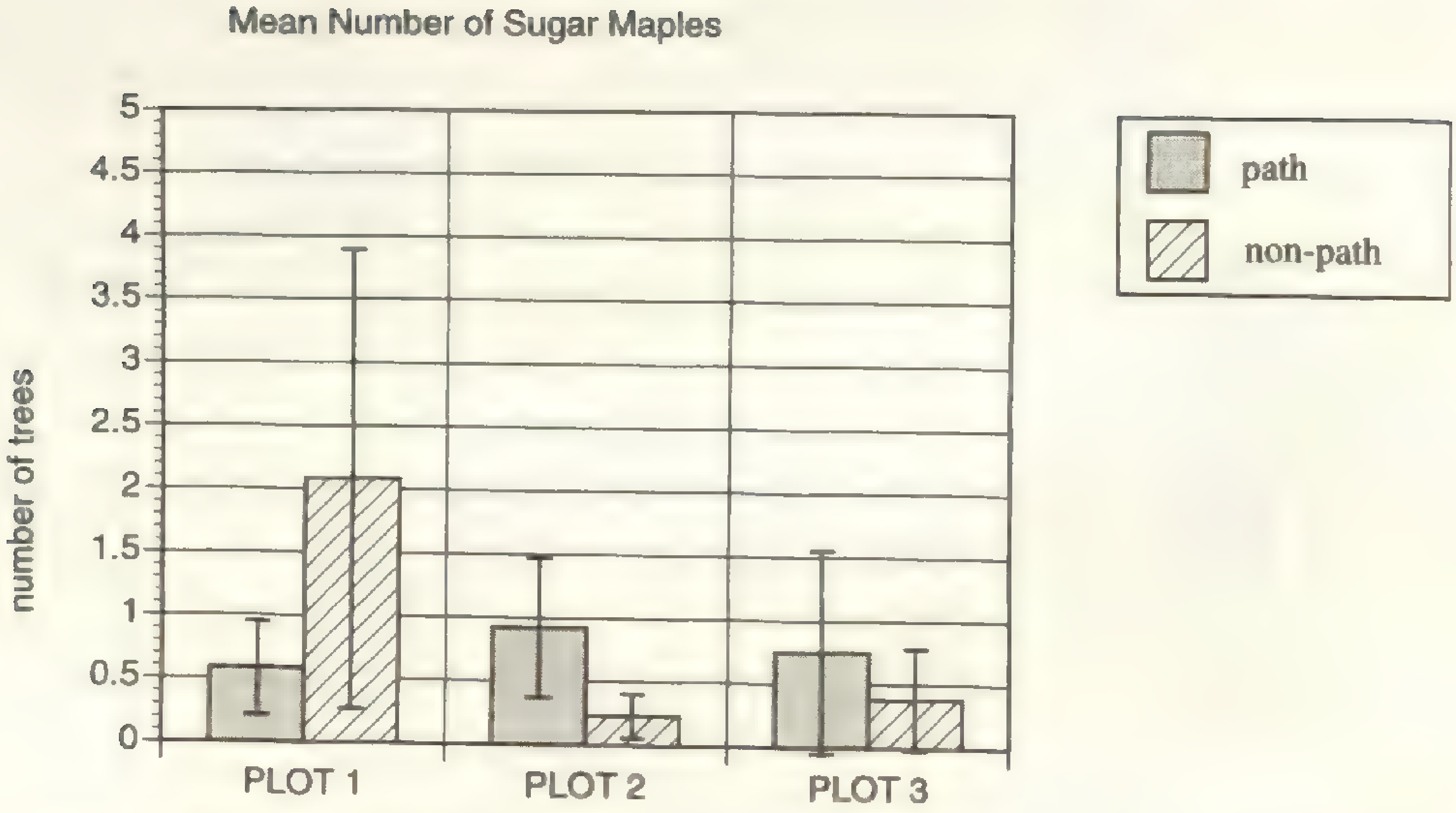

Figure 3. Mean number of sugar maples in plots 1–3 at the Middlesex Fells Reservation. Error bars indicate ±1 SE.

pend on disturbance for successful invasion favor the second pattern. These species also share many characteristics of early-successional plants, such as high rates of population growth, photosynthesis, respiration, transpiration, and growth (Bazzaz 1986). In this study, there were often large numbers of Norway maples near the road, but they penetrated further into the forest with large spaces in-between, not in a solid front. In comparison to sugar maple (Kloeppel and Abrams 1995), Norway maple has many of the characteristics listed by Bazzaz that would make it better adapted than sugar maple to exploit disturbance.

Norway maple may be contributing to a proposed trend of invasion by exotics and loss of native species in the Middlesex Fells. A survey of species lost over one hundred years found three trends: the number of native species declined, the number of exotics increased in proportion to the total flora, and species were most affected in moist habitats (Drayton and Primack 1996). This suggests several effects Norway maple could have in the Fells. For example, in this study, I observed that Norway maple invaded furthest in low, moist areas, which may lead to its contributing to any loss of native species in the moist areas. As Norway maple also has a lower species diversity under its canopy than sugar maple (Wyckoff and Webb 1996), this may also influence the Middlesex Fells' herbaceous layer in the moister areas.

As a common street tree, Norway maple has great invasive potential. The likelihood of successful invasion depends on the nature and extent of the disturbance, the number of exotic seeds deposited each year, and how long the community is subject to the propagules (Rejmanek 1989). Thus, communities near street-planted Norway maples are at high risk of invasion. First, the street is a large disturbance, producing an edge effect and introducing pollution and road salt into the community. Second, the woodland is subjected to an annual deposition of seeds from mature Norway maple trees. Since Norway maple is widely planted, many communities are exposed to its seeds. Where the habitat is not conducive to invasion, the threat may not materialize, but having it planted so widely increases the chance that a vulnerable community will be nearby.

Since Norway maple is becoming established in the Fells, and becoming the dominant tree near the road at many sites, it would be worthwhile to investigate other species in the Fells that might be influenced by Norway maples' dense stands. It may be reasonable to cut down the roadside trees that are the seed source, replacing them with a native tree such as sugar maple. It is especially important to remove those trees in the Fells that are in sensitive areas. These results also support restrictions on further path construction for recreational purposes.

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# *CARDAMINE GEORGIANA* (BRASSICACEAE), A NEW NAME REPLACING *DENTARIA MICROPHYLLA*

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ABSTRACT. *Cardamine georgiana* is proposed to replace the illegitimate name *C. microphylla* (Willd.) O. E. Schulz (1903; *non* Adams 1817). A discussion on the generic limit of *Cardamine* including *Dentaria* is presented.

Key Words: *Cardamine*, *Dentaria*, Georgia

Both *Cardamine* and *Dentaria* were simultaneously published by Linnaeus (1753). When uniting the two genera, Crantz (1769) adopted *Cardamine* for the combined genus and, therefore, this name has priority (Greuter et al. 1994; Article 11.5 ex. 14). Although in most treatments (Akeroyd and Marhold 1993; Al-Shehbaz 1988; Cullen 1965; Rollins 1993; Schulz 1903, 1936) *Dentaria* is reduced to a synonym of *Cardamine*, some North American authors (Detling 1936; Harriman 1965; Turrill et al. 1994) and eastern European authors (Busch 1909, 1939; Czerepanov 1995; Grossheim 1950; Khintibidze 1979) maintain it as a distinct genus.

The alleged morphological differences between *Dentaria* (larger flowers, fleshier and larger rhizomes, often petiolate cotyledons, and stems narrowest at base) and *Cardamine* (usually smaller flowers, often nonfleshy and smaller rhizomes, usually sessile cotyledons, and stems usually broadest at base) clearly do not hold if the two genera are examined on a worldwide basis (Al-Shehbaz 1988). As indicated by Franzke et al. (1998) and Sweeney and Price (pers. comm.), molecular data clearly show that *Dentaria* is polyphyletic and is nested within *Cardamine*.

During the process of compiling a worldwide checklist of chromosome numbers of the Brassicaceae (Cruciferae), it became evident that the transfer by Schulz (1903) of *Dentaria microphylla* Willd. to *Cardamine* created a later homonym of *C. microphylla*

Adams and two other homonyms (see below). Therefore, *C. georgiana* is proposed as a *nom. nov.* to replace the illegitimate name.

*Dentaria microphylla* which is narrowly endemic to Georgia and adjacent easternmost Turkey, was recognized in *Dentaria* by Busch (1909, 1939), Czerepanov (1995), Grossheim (1950), and Khintibidze (1979) under this correct name. It was treated in *Cardamine* by Cullen (1965), Kolakovsky (1982), and Schulz (1903) under the illegitimate later homonym *C. microphylla* (Willd.) O. E. Schulz. By contrast, the earlier homonym *C. microphylla* Adams is a species distributed in northwestern Alaska, the Russian Far East, and eastern Siberia (Berkutenko 1988; Czerepanov 1995; Khatri 1990; Rollins 1993).

**Cardamine georgiana** Al-Shehbaz & Warwick, *nom. nov.* Replaced name: *Dentaria microphylla* Willdenow, Sp. Pl. 3: 479. 1800. Syn. *Cardamine microphylla* (Willd.) O. E. Schulz, Bot. Jahrb. Syst. 32: 342. 1903, not *C. microphylla* Adams, Mém. Soc. Imp. Naturalistes Moscou 5: 111. 1817, not *C. microphylla* J. Presl, Delic. Prag. 1: 15, 1822. TYPE: [GEORGIA]. Collector and locality unknown (HOLOTYPE: B not seen).

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# COVARIANCE OF LICHEN AND VASCULAR PLANT FLORAS

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ABSTRACT. The geographic relationships among taxonomic groups are important to study to determine patterns of biodiversity and whether or not associations occur between large groups, e.g., birds and vascular plants. This study was undertaken to determine relationships between higher plants and lower plants, specifically vascular plant and lichen floras in nine national parks of the Great Lakes region. No significant relationship was found between vascular plant floras and lichen floras in this area, which spans 1200 km longitudinally, or between an additional 19 areas from North America that were less than 1000 km$^2$ in area. For areas larger than 1000 km$^2$, however, a significant positive relationship existed for 33 areas that span one to approximately 150 million km$^2$. The ratio of numbers of vascular plants to lichens appeared to average just over 6 across the 33 areas. In the Great Lakes parks, between 28–30% of either the vascular plant or lichen species were singletons (occurring in only one park), but the parks that contained the most singletons were not congruent: Isle Royale had the most singleton lichens, while Indiana Dunes had the most vascular plant singletons. Fewer lichen species (2%) than vascular plants (4%) occurred in all nine parks. Latitude appeared to explain some of the variation between the two groups: vascular plants decreased with increasing latitude, while lichens increased.

Key Words: floras, lichens, vascular plants, species-area curves

The number of lichen species in North America, north of Mexico, is thought to be approximately 3600 (Esslinger and Egan 1995), while the number of vascular plant species approaches 22,000 (Kartesz 1994), a ratio of about six vascular plant species to one lichen species. Although general, ratios like this have been used to make broad biodiversity estimates (e.g., Hawksworth 1991). Such estimates can be made more useful if the geographic pattern of covariance of higher taxa can be ascertained. In recent years studies of spatial covariance of higher taxa have been conducted in order to determine patterns of biodiversity hotspots, or the relationships among taxa, if any exist (Faith and Walker 1996; Gaston 1996). Many factors can affect spatial covariance, including scale, environmental factors, and biological properties of the taxa. Several authors have pointed out that lichen and vascular plant diversities may not track each other in general due to climate (Huston 1994) and habitat diversity (Galloway 1992; Gilbert 1977). Another study found that lichen biodiversity decreased significantly with an increase in vascular plant cover (Pharo and Beattie 1997). In addition, we suspected that the effects of air pollutants may also be a factor affecting lichen and vascular plant floras differentially because of the greater air pollution sensitivities of lichens. This paper explores all of these issues using the lichen and vascular plant floras of nine national parks in the Great Lakes region of the United States.

The lichen floras of nine national parks in the Great Lakes region of the north central United States have been well studied in recent years and are considered to be fairly complete. The parks include Apostle Islands National Lakeshore in Wisconsin (APIS), Cuyahoga Valley National Recreation Area in Ohio (CUVA), Grand Portage National Monument in Minnesota (GRPO), Indiana Dunes National Lakeshore in Indiana (INDU), Isle Royale National Park (ISRO) and Pictured Rocks National Lakeshore in Michigan (PIRO), St. Croix National Scenic River in Minnesota and Wisconsin (SACN), Sleeping Bear Dunes National Lakeshore in Michigan (SLBE), and Voyageurs National Park in Minnesota (VOYA; Figure 1). It is logical to study these floras because they should show affinities with one another, being associated geographically within the homogeneous Great Lakes/north central U. S. region. The nine parks span a region of about 1200 km longitudinally, and in the aggregate, cover a total area of 201,000 km$^2$. The vascular plant floras of these parks have been studied and were segregated into two groups by multivariate analyses (Bennett 1996a, 1996b). This study was also undertaken to determine if the same groups of parks are segregated based on the lichen floras.

The management of natural area preserves is sometimes focused on a select group of organisms, e.g., mammals, trees, rare plants, birds, or butterflies. It is often implicit in the management of these groups that the management of one group will also satisfactorily manage another group by association. This is because it is assumed that the biological groups in an area are related. For

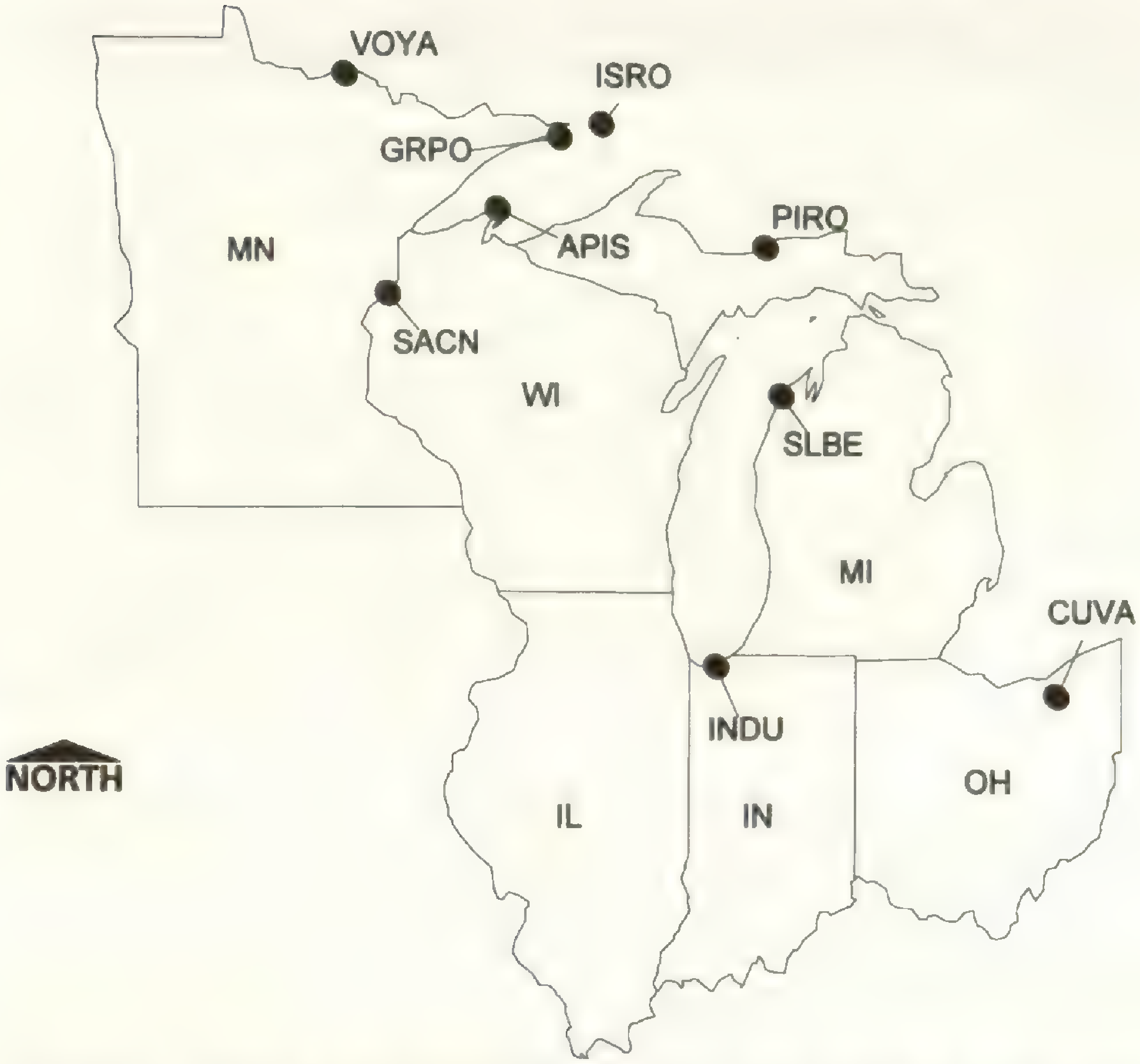

Figure 1. Map of nine Great Lakes national park units for which floras were used in this study. Park codes are explained in the introduction.

the purposes of this study, it was assumed that vascular plants and lichens are related floristically somehow, although ecologically they occupy habitats at very different scales and their floristic relationships may be obscure. From a management perspective however, it may be assumed that if there are more vascular plants in an area there will also be more lichens. This study was undertaken in order to determine the validity of this assumption by attempting to prove the hypothesis that there is no relationship between vascular plant and lichen floras.

## MATERIALS AND METHODS

Lichen floristic field work in the nine parks was conducted during the summer in the years from 1978 to 1995, although collecting was not done in these particular parks every year (Wet-

Table 1. Numbers of collections, collecting days, and collection localities for lichens in nine Great Lakes national parks. See introduction for park names.

| | Number of | | |
|---|---|---|---|
| Park | Collections | Collecting Days | Collection Localities |
| APIS | 1497 | 21 | 28 |
| CUVA | 304 | 11 | 31 |
| GRPO | 373 | 3 | 6 |
| INDU | 371 | 14 | 24 |
| ISRO | 5246 | 53 | 72 |
| PIRO | 1231 | 11 | 25 |
| SACN | 2327 | 88 | 77 |
| SLBE | 847 | 10 | 27 |
| VOYA | 8028 | 80 | 128 |

more 1983b, 1985, 1988a, 1988b, 1989, 1990a, 1990b, 1991, 1992b; Wetmore and Bennett 1996 [data are available on the Internet at www.ies.wisc.edu/brd]). Collection localities in each park were selected to include all habitats and vegetation types. The collection localities were distributed over the entire park, and vegetation types were studied multiple times. At each locality, all groups of lichens were collected (fruticose, foliose, squamulose, and crustose) and sufficient time was spent examining all substrates. At each locality all species found were collected to provide relative abundance estimates, even though the same species might have been found at previous localities. A summary of the collecting efforts is shown in Table 1. Vascular plant floras and methods were described previously (Bennett 1996a).

The nomenclature of each lichen flora was updated to the fifth checklist (Egan 1987) so as to standardize all the names. The names were then entered into a computer spreadsheet program (MICROSOFT EXCEL, Microsoft Corp., Seattle, WA) and the presence/absence of each species recorded in a field for each park. Various tallies and sorts were performed in order to perform quality control procedures and to rank species by frequencies. This file was also used to analyze the data statistically, using MINITAB (Minitab, State College, PA) and SYSTAT (SPSS, Chicago, IL). Relationships between variables were tested with Pearson's linear correlation coefficients.

Similarities between park floras were calculated using Jaccard's

Table 2. Area, numbers of lichen and vascular plant species, average Jaccard similarity based on lichens and vascular plants, and average distance from the other parks for nine Great Lakes national parks. See introduction for park names.

| Park | Area (km²) | Latitude (decimal degrees N) | Number of Species | | Average Similarity | | Average Distance (km) |
|---|---|---|---|---|---|---|---|
| | | | Lichen | Vascular Plant | Lichen (%) | Vascular Plant (%) | |
| APIS | 6605 | 47.000 | 285 | 509 | 39 | 35 | 388 |
| CUVA | 3136 | 41.283 | 66 | 855 | 18 | 26 | 842 |
| GRPO | 287 | 47.967 | 182 | 279 | 30 | 23 | 383 |
| INDU | 5203 | 41.625 | 62 | 1399 | 19 | 28 | 638 |
| ISRO | 54,140 | 48.000 | 554 | 698 | 31 | 37 | 400 |
| PIRO | 25,545 | 46.567 | 245 | 723 | 36 | 39 | 415 |
| SACN | 26,459 | 46.000 | 282 | 1165 | 34 | 33 | 443 |
| SLBE | 23,663 | 44.875 | 182 | 928 | 33 | 37 | 426 |
| VOYA | 55,955 | 48.500 | 458 | 603 | 35 | 35 | 566 |

similarity index, which measures the proportion of park pairs where species are present in both parks in the pair. Details are given in Bennett (1996b). The correlation of two similarity matrices was tested with Mantel's test with PC-ORD (McCune and Mefford 1997).

Park distances and latitudes were measured using STREET ATLAS (De Lorme, Freeport, ME), a desktop computer mapping program. Straight line distances and latitudes were calculated using the approximate park centroids for park locations. Distances were rounded to the nearest five kilometers.

## RESULTS

A floristic summary of each park is shown in Table 2. Isle Royale had the greatest number of lichen species, while Indiana Dunes had the lowest. The greatest and lowest numbers of vascular plant species, however, were at Indiana Dunes and Grand Portage, respectively. Based on the lichen floras, seven of the parks were, on average, between 30 and 40% similar to all the other parks, except for Indiana Dunes and Cuyahoga Valley, which were almost 20% similar to all other parks. This is not too surprising, given that on average they are farther away from all the other parks. Overall similarity based on vascular plant floras followed the same pattern, except for Grand Portage, which had the lowest overall similarity, lower than Cuyahoga Valley and Indiana Dunes.

Some of the variables were significantly correlated (Table 3): lichen numbers and park area (Figure 2), and average lichen similarity and average distance (Figure 3) or latitude were the strongest relationships. Number of lichens increased with latitude, while vascular plant numbers decreased (Figure 4). Numbers of lichens and vascular plants appeared to be negatively correlated, but the probability of the correlation occurring by chance was high (0.33). Park similarities based on lichens and vascular plants were comparable ($P = 0.0517$). Vascular plant similarity significantly increased with area and did not appear related to latitude, while park lichen similarity increased with latitude and was not related to area.

The lichen flora Jaccard similarity matrix for all possible 36 pairs of the nine parks is shown in Table 4. Two park pairs, Isle Royale and Voyageurs, and Apostle Islands and Pictured Rocks were greater than 50% similar, while the overall average was 31%. The comparable distance matrix (Table 5) shows that Cuyahoga Valley and Voyageurs are just over 1200 km apart, while Grand Portage and Isle Royale are the closest pair at only 60 km apart. The similarities for these same pairs were 11% and 30%, respectively (Table 4). When all 36 pairs of similarities and distances were plotted against each other (Figure 5), there was a clear negative relationship, even though the maxima and minima did not all correspond.

The overall average of vascular plant similarities was 32% (see Table 1 in Bennett 1996b), and only one park pair, Isle Royale and Pictured Rocks, was more than 50% similar. The similarities of Cuyahoga Valley and Voyageurs, and Grand Portage and Isle Royale were 23% and 30%, respectively. The overall vascular plant similarity matrix was significantly positively related to the lichen similarity matrix (Mantel $r = 0.9151$, $t = 6.3718$, $P = 0.0000$), suggesting that these parks show comparable degrees and patterns of similarity based on both vascular plant and lichen floras.

A cluster analysis of the lichen flora Jaccard similarity matrix did not reveal any significant groupings because the similarities were not very diverse. However, a cluster analysis of the presence/absence matrix of all species in the nine parks did reveal

Table 3. Pearson's linear correlation coefficients for variables given in Table 2. Significance levels of coefficients are indicated by preceding asterisks: * (0.05), ** (0.01), and *** (0.001). [1] Number of species.

| | Area | Latitude | Lichens[1] | Vascular Plants[1] | Average Lichen Similarity | Average Vascular Plant Similarity |
|---|---|---|---|---|---|---|
| Latitude | 0.5702 | | | | | |
| Lichens[1] | ***0.9124 | **0.7968 | | | | |
| Vascular plants[1] | −0.1671 | *−0.6985 | −0.3715 | | | |
| Average lichen similarity | 0.5214 | **0.8379 | 0.6210 | −0.4850 | | |
| Average vascular plant similarity | *0.7054 | 0.3882 | 0.5783 | 0.0440 | 0.6628 | |
| Average distance | −0.2143 | *−0.7685 | −0.4796 | 0.4002 | **−0.8083 | −0.4540 |

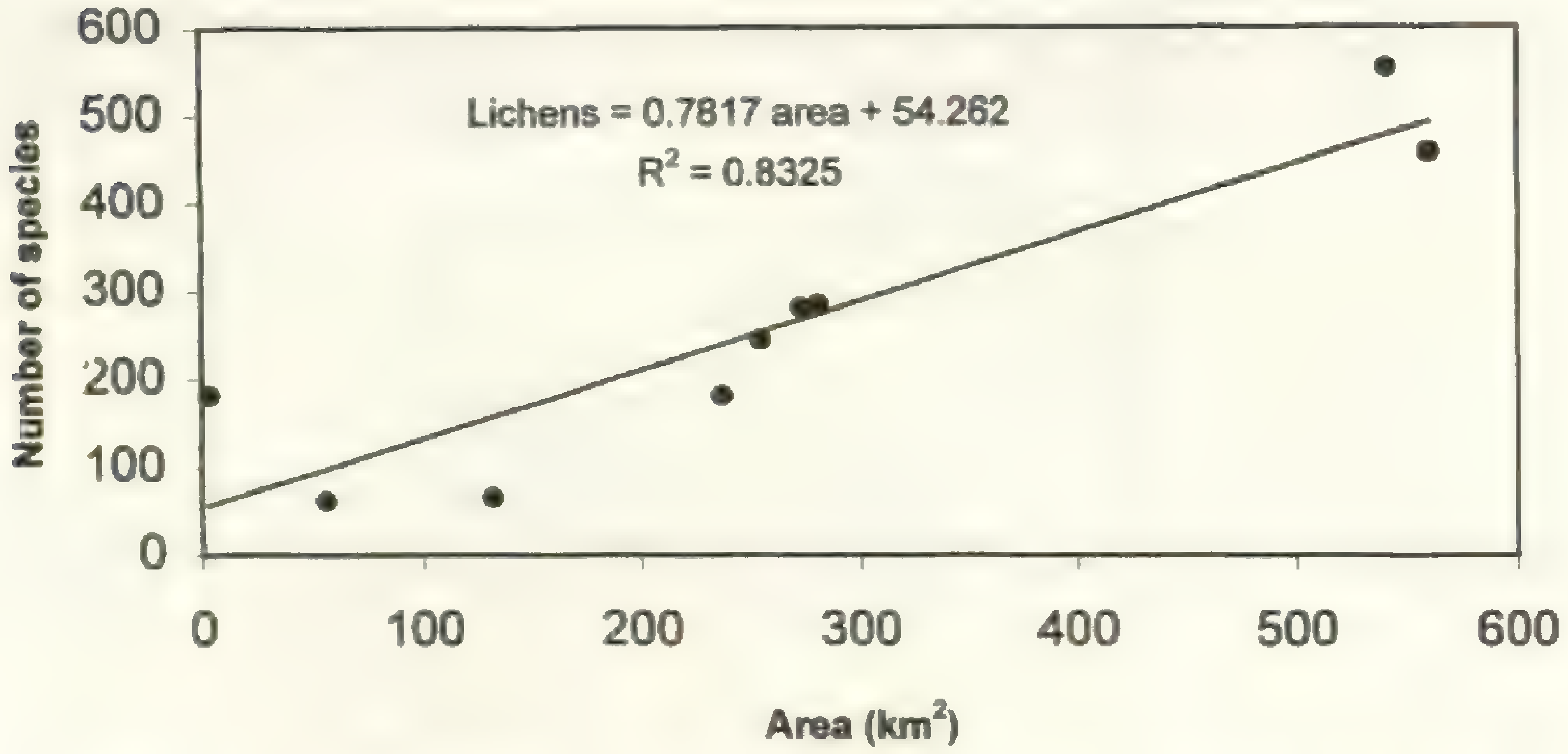

Figure 2. Relationship between number of lichen species and area for nine Great Lakes national parks, and fitted linear regression line.

some interesting groups (Figure 6). At the highest similarity level, about 80%, four parks (Apostle Islands and Pictured Rocks, and Cuyahoga Valley and Indiana Dunes) were grouped into two pairs that were themselves only about 36% similar. Cuyahoga Valley and Indiana Dunes appeared to be two parks that were unrelated floristically to the other seven, which appeared to be about 50% similar overall. Isle Royale, however, was less similar to the other six northern parks, in spite of the high individual Jaccard similarity with Voyageurs. Two groups of three parks each had sim-

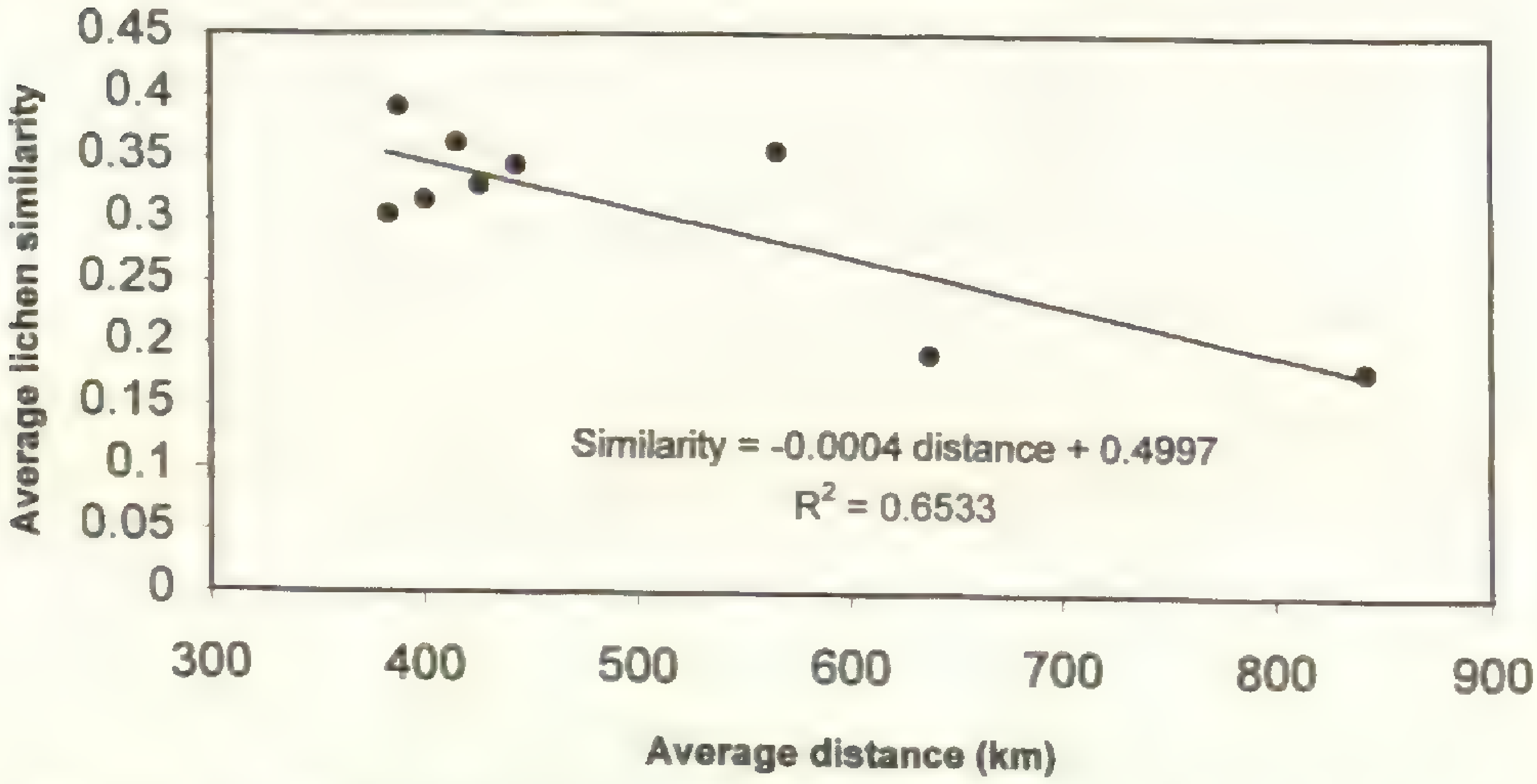

Figure 3. Relationship between average lichen flora similarity and average distance from the other parks for the nine Great Lakes national parks, and fitted linear regression line.

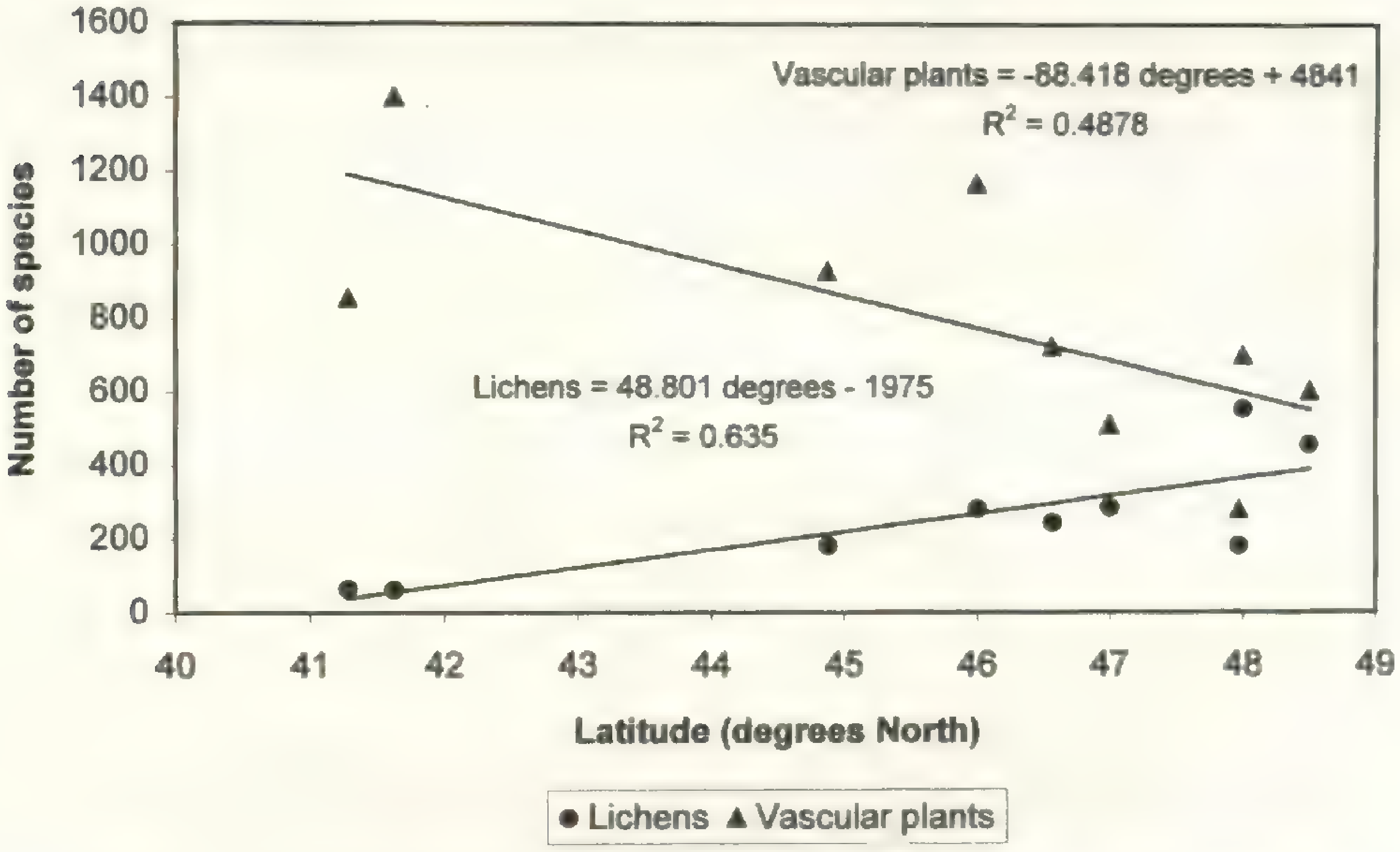

Figure 4. Relationships between number of vascular plant and lichen species and latitude for nine Great Lakes national parks, and fitted linear regression lines.

ilarities of 60–70%. One of these had two parks on the southern shore of Lake Superior and one at the northern end of Lake Michigan (Apostle Islands, Pictured Rocks, and Sleeping Bear Dunes), and the other consisted of three Minnesota parks (Grand Portage, Voyageurs, and St. Croix).

Totals of 698 lichen species in 162 genera were found in the nine parks when the floras were aggregated. The most frequent species, i.e., those that were found in all nine parks (14 species, or 2% of all lichen species found), included *Arthonia caesia, Candelariella efflorescens, Cladina rangiferina, Cladonia chlo-*

Table 4. Jaccard similarity (%) matrix for lichen floras of nine national parks.

| | APIS | CUVA | GRPO | INDU | ISRO | PIRO | SACN | SLBE |
|---|---|---|---|---|---|---|---|---|
| CUVA | 14.3 | | | | | | | |
| GRPO | 43.7 | 13.2 | | | | | | |
| INDU | 16.4 | 43.8 | 14.0 | | | | | |
| ISRO | 44.7 | 9.0 | 30.0 | 9.0 | | | | |
| PIRO | 57.3 | 13.1 | 40.9 | 15.0 | 38.2 | | | |
| SACN | 43.5 | 20.0 | 33.7 | 19.0 | 36.4 | 37.2 | | |
| SLBE | 42.8 | 20.4 | 31.9 | 25.1 | 25.8 | 45.7 | 39.8 | |
| VOYA | 49.8 | 11.0 | 35.6 | 11.1 | 59.1 | 41.7 | 45.7 | 30.6 |

Table 5. Distance matrix for nine national parks. Distances are in kilometers between park centroids.

| | APIS | CUVA | GRPO | INDU | ISRO | PIRO | SACN | SLBE |
|---|---|---|---|---|---|---|---|---|
| CUVA | 950 | | | | | | | |
| GRPO | 145 | 975 | | | | | | |
| INDU | 670 | 470 | 745 | | | | | |
| ISRO | 185 | 930 | 60 | 725 | | | | |
| PIRO | 340 | 690 | 300 | 560 | 250 | | | |
| SACN | 125 | 980 | 275 | 620 | 320 | 435 | | |
| SLBE | 425 | 530 | 300 | 390 | 410 | 185 | 480 | |
| VOYA | 260 | 1210 | 260 | 920 | 320 | 560 | 310 | 685 |

*rophaea, C. coniocraea, C. cristatella, Flavoparmelia caperata, Lepraria finkii, Melanelia subaurifera, Parmelia sulcata, Phaeophysica pusilloides, Physconia detersa, Punctelia rudecta,* and *Scoliciosporum chlorococcum.* Thirty percent of lichens (210 species) occurred in only one park. Most of these (129) occurred in Isle Royale. For the vascular plants, an aggregated flora of 2102 species in 691 genera was found over all the parks, with 81 (4%) occurring in all nine parks. Twenty-eight percent of the vascular

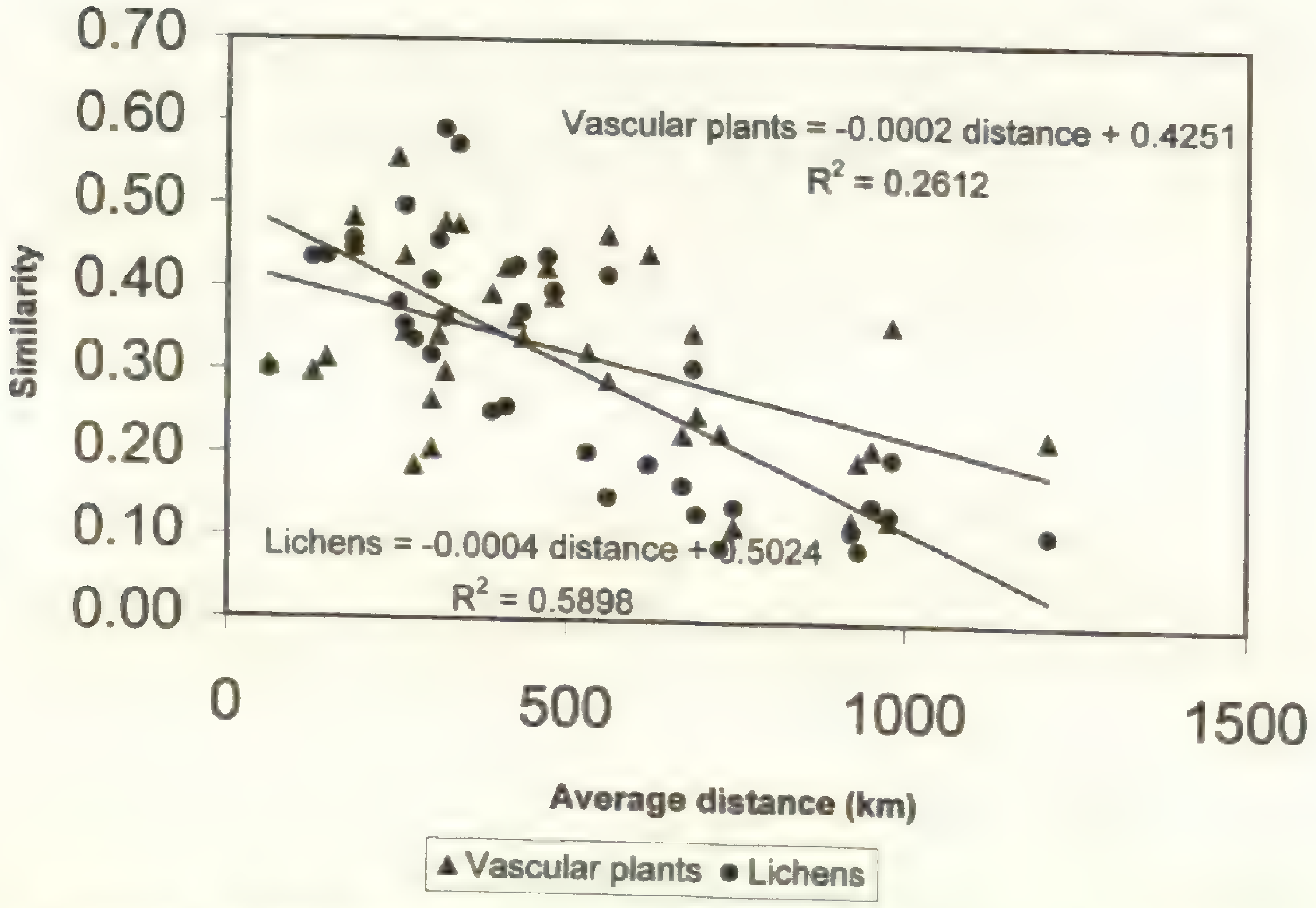

Figure 5. Relationships of vascular plant and lichen flora similarities to distance between parks for each of the 36 possible park pairs of the nine Great Lakes national parks, and fitted regression lines.

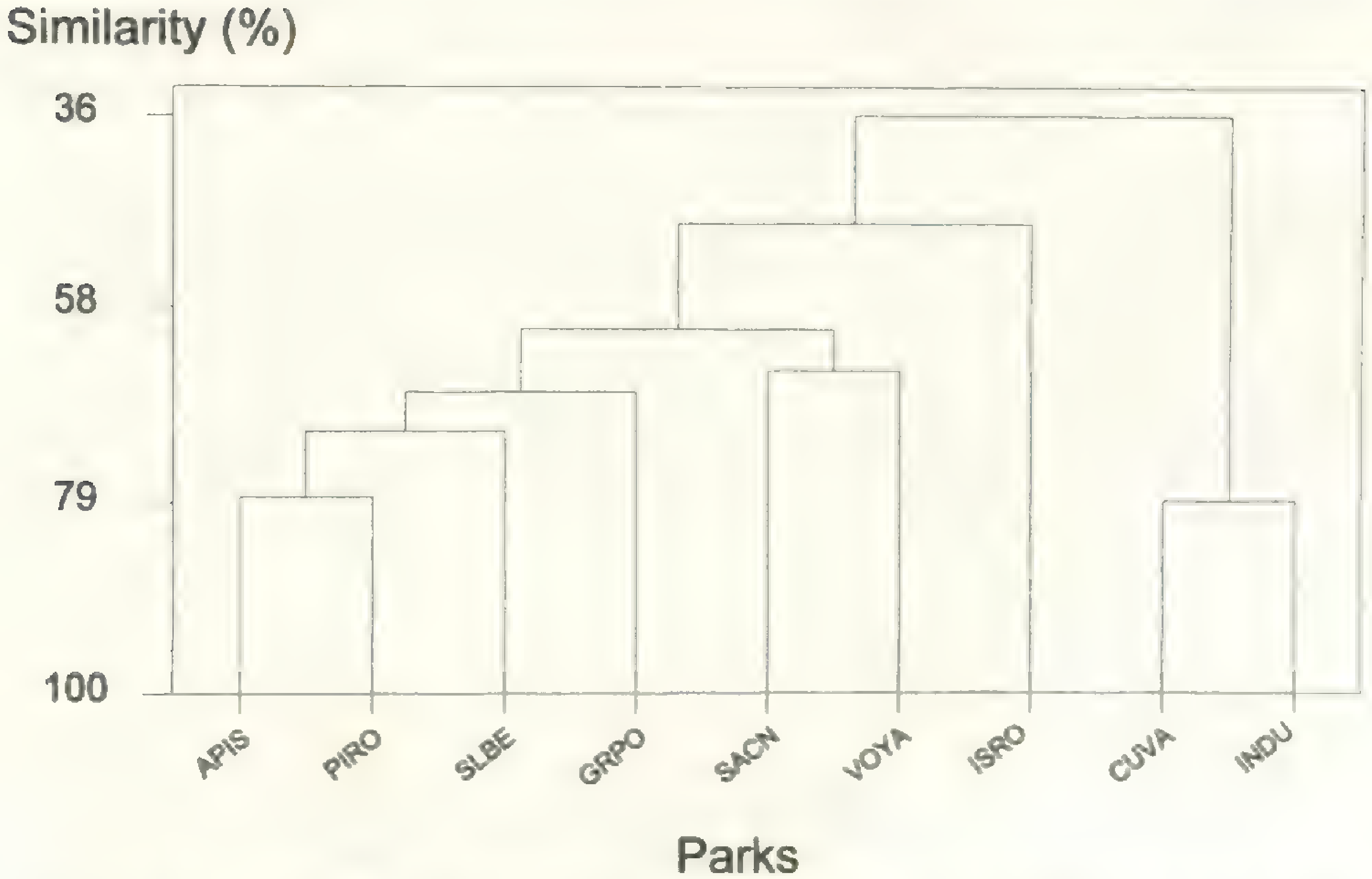

Figure 6. Cluster dendrogram for nine Great Lakes national park lichen floras, using Ward's linkage and correlation for the distance measure.

plants (596 species) occurred in just one park each. Most of these (221) were found in Indiana Dunes.

## DISCUSSION

At first glance it appears that for this set of nine park floras there was no obvious relationship between vascular plants and lichens. However, further examination of the parks sheds more light on the problem. Two parks, Cuyahoga Valley and Indiana Dunes, are in locations that have been subject to oxidant and sulfur oxide pollution fumigations for many years, and studies have shown that the lichen floras of these parks have decreased to about 80% of their historical floras (Wetmore 1988a, 1989). However, if these two parks were to be omitted from the analysis there would not be enough data points to draw justifiable conclusions about the vascular plant/lichen relationship. When the historical total numbers of species were used instead of current species numbers (205 for Cuyahoga Valley and 154 for Indiana Dunes), there was still no clear relationship. This appears due to the vascular plant flora numbers rather than the lichen flora numbers. The vascular plant flora numbers were not linearly related to area (Table 3). This is probably due to confounding effects of

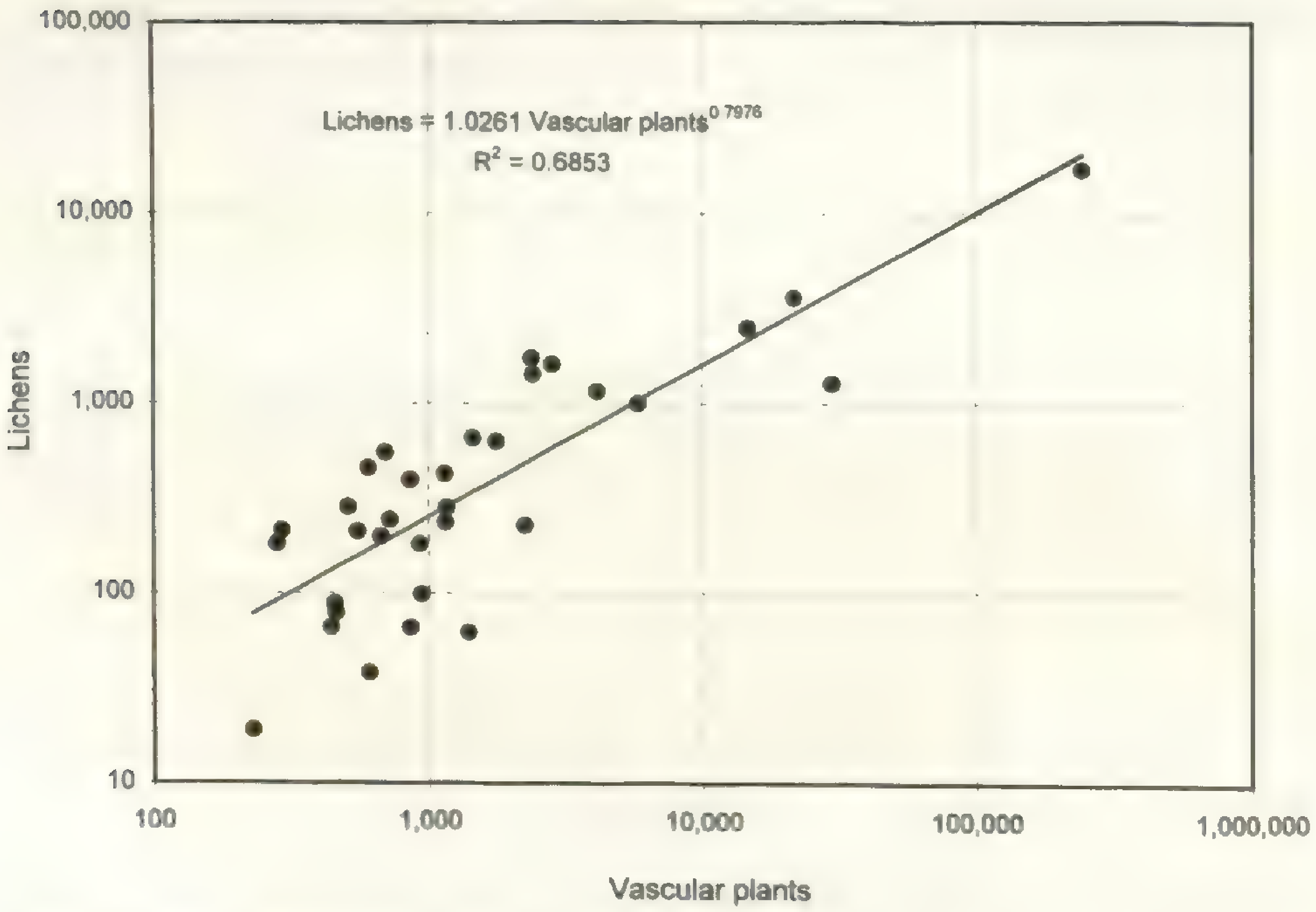

Figure 7. Relationship between numbers of lichen and vascular plant species for 33 areas, and fitted non-linear regression line.

latitude, as vascular plant diversity decreases with increasing latitude, the opposite of what happens with the lichen diversity (Huston 1994).

Do lichen and vascular plant floras co-vary? At the scale of the Great Lakes no relationship could be seen, but what about at other scales? The flora data for the nine parks were combined with comparable data for 24 other geographic areas, including the world, and are shown in Figure 7 (Table 6). It appears that when larger geographic areas were included, a significant, positive relationship was found between the two floras ($r$ = 0.9808), even when the floras of the world were omitted ($r$ = 0.7037). When only areas less than 1000 km$^2$ were considered, the relationship broke down (r = 0.0896). Area was obviously a factor when all 33 areas were considered (Figure 8), but may not have been with areas under 1000 km$^2$ for the reasons given above. This finding differs significantly from an older study of lichens and area where no relationship was found above 1000 km$^2$ (Wetmore 1967), which was based on incomplete inventories.

We conclude that any relationship between vascular plant and lichen floras is scale-dependent. For natural areas under approximately 1000 km$^2$, no relationship was found for the national

Table 6. Areas, numbers of vascular plant (VP) and lichen (L) species, and the ratio of the two (VP/L), for 33 locations.

| Location | Area ($km^2$) | Vascular Plants | Lichens | VP/L | Reference and Comment |
|---|---|---|---|---|---|
| Homestead National Monument, NE | 1 | 227 | 19 | 11.95 | Bennett 1996a; Wetmore and Bennett 1997 |
| George Washington Carver National Monument, MO | 1 | 605 | 38 | 15.92 | Bennett 1996a; Wetmore 1992a |
| Pipestone National Monument, MN | 1 | 439 | 66 | 6.65 | Bennett 1996a; Wilson and Vinyard 1986 |
| Grand Portage National Monument, MN | 3 | 279 | 182 | 1.53 | Bennett 1996a; Wetmore 1992b |
| Effigy Mounds National Monument, IA | 6 | 458 | 79 | 5.80 | Bennett 1996a; Wetmore and Bennett 1997 |
| Wilson's Creek National Battlefield, MO | 7 | 454 | 88 | 5.16 | Bennett 1996a; Wetmore and Bennett 1997 |
| Tuxedni Wilderness, AK | 23 | 290 | 214 | 1.36 | Talbot et al. 1995; Talbot et al. 1992 |
| Indiana Dunes National Lakeshore, IN | 52 | 1399 | 62 | 22.56 | Bennett 1996a; Wetmore 1988a |
| Apostle Islands National Lakeshore, WI | 66 | 509 | 285 | 1.79 | Bennett 1996a; Wetmore 1990a |
| Cuyahoga Valley National Recreation Area, OH | 131 | 855 | 66 | 12.95 | Bennett 1996a; Wetmore 1989 |

Table 6. Continued.

| Location | Area (km²) | Vascular Plants | Lichens | VP/L | Reference and Comment |
|---|---|---|---|---|---|
| Nantucket Island, MA | 140 | 939 | 99 | 9.48 | Dunwiddie and Sorrie 1996 (species not seen after 1960 omitted) |
| Acadia National Park, ME | 190 | 858 | 397 | 2.16 | Anonymous 1997b; Wetmore 1984 |
| Sleeping Bear Dunes National Lakeshore, MI | 237 | 928 | 182 | 5.10 | Bennett 1996a; Wetmore 1988b |
| Pictured Rocks National Lakeshore, MI | 255 | 723 | 245 | 2.95 | Bennett 1996a; Wetmore 1990b |
| St. Croix National Scenic Riverway, MN and WI | 265 | 1165 | 282 | 4.13 | Bennett 1996a; Wetmore 1991 |
| Theodore Roosevelt National Park, ND | 285 | 550 | 212 | 2.59 | Anonymous 1997b; Wetmore 1983a |
| Chiricahua National Monument, AZ | 485 | 672 | 200 | 3.36 | Anonymous 1997b; Wetmore and Bennett 1992 (Lichen number is doubled because flora is 50% known.) |
| Isle Royale National Park, MI | 541 | 698 | 554 | 1.26 | Bennett 1996a; Wetmore 1985 |
| Voyageurs National Park, MN | 560 | 603 | 458 | 1.32 | Bennett 1996a; Wetmore 1983b |

Table 6. Continued.

| Location | Area (km²) | Vascular Plants | Lichens | VP/L | Reference and Comment |
|---|---|---|---|---|---|
| Glacier National Park, MT | 4,102 | 1147 | 425 | 2.70 | Anonymous 1997b; Debolt and McCune 1993 |
| Yellowstone National Park, WY | 8,983 | 1150 | 236 | 4.87 | Anonymous 1997b; Eversman 1990 |
| Israel | 21,946 | 2250 | 229 | 9.83 | Zohary 1962; Kondratyuk et al. 1996 |
| Netherlands | 41,784 | 1781 | 633 | 2.81 | Statistics Netherlands 1997; B. Wit, pers. comm. |
| Tasmania | 67,858 | 1456 | 655 | 2.22 | Chapman 1997; Galloway 1992 |
| United Kingdom | 229,979 | 2397 | 1,730 | 1.39 | Palmer 1996; Galloway 1992 |
| New Zealand | 268,114 | 4167 | 1,162 | 3.59 | Allan 1961; Moore and Edgar 1970; Healy and Edgar 1980; Webb et al. 1988; Galloway 1985 |
| Finland | 338,148 | 2423 | 1,420 | 1.71 | Anonymous 1997a; O. Vitkainen, pers. comm. 1997 |

Table 6. Continued.

| Location | Area (km²) | Vascular Plants | Lichens | VP/L | Reference and Comment |
|---|---|---|---|---|---|
| California | 411,049 | 5862 | 1,000 | 5.86 | Hickman 1993; Tucker and Jordan 1979 |
| British Columbia | 948,600 | 2850 | 1,600 | 1.78 | British Columbia Ministry of Environment, Land, and Parks 1997 |
| Australia | 7,682,341 | 14,679 | 2,499 | 5.87 | Chapman 1997; Galloway 1992 |
| China | 9,596,961 | 30,000 | 1,274 | 23.55 | Harvard University Herbaria 1997; Wei 1991 |
| United States and Canada | 21,479,211 | 21,757 | 3,600 | 6.04 | Kartesz 1994; Esslinger and Egan 1995 |
| World | 149,702,000 | 243,893 | 17,000 | 14.35 | Mabberley 1987; Thorne 1992; Galloway 1992 |

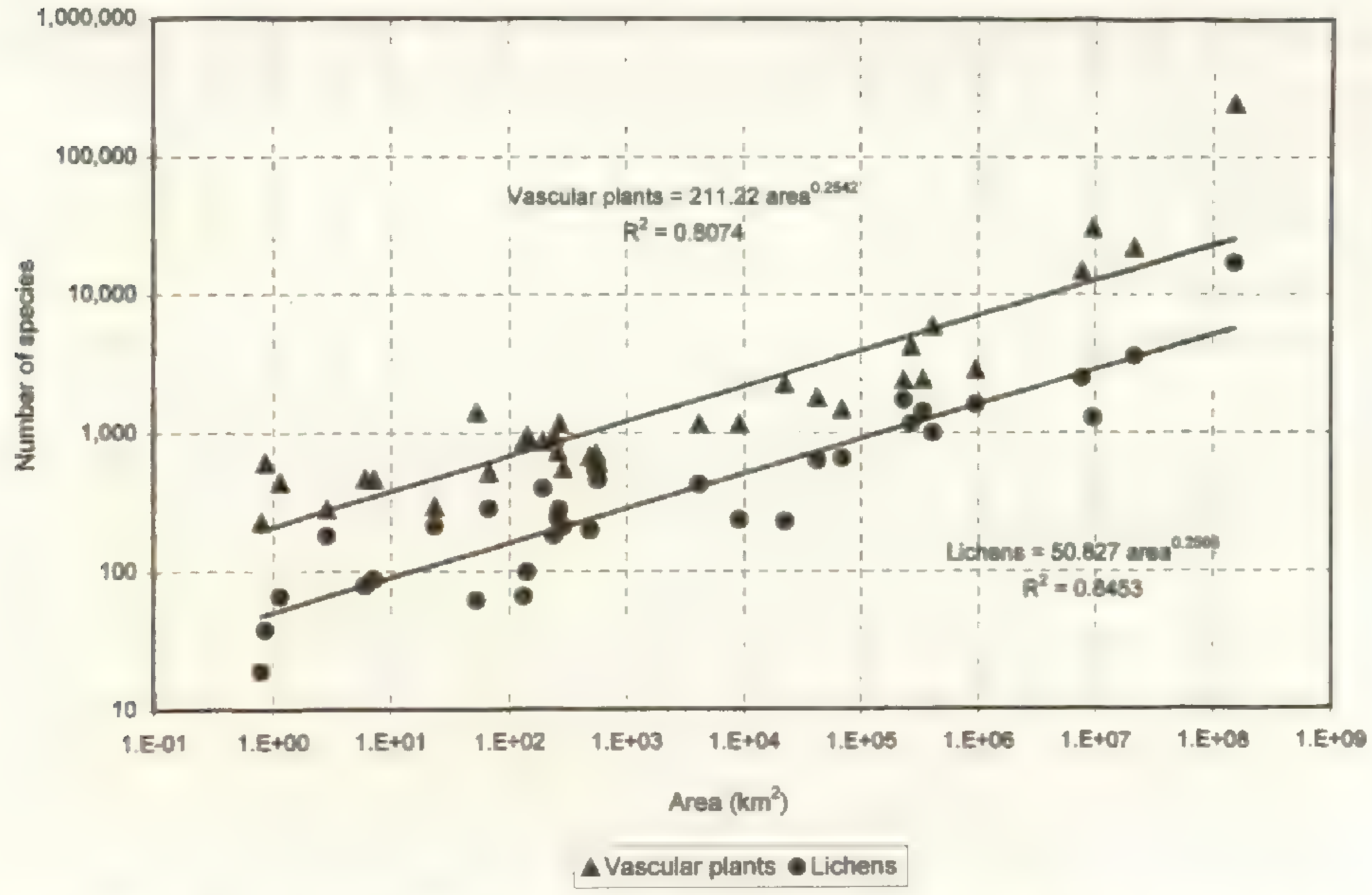

Figure 8. Relationships between numbers of lichen and vascular plant species and area for 33 areas, and fitted non-linear regression lines.

parks and areas in this study. This is partly due to the confounding effect of latitude, which affects vascular plant and lichen richness in opposite ways. A second reason is that we deliberately chose a set of natural areas in a relatively homogeneous ecological region so as not to introduce significant habitat diversity. The third reason is that vascular plants and lichens occupy microhabitats that are unrelated because of the scale differences between the two groups of plants. Lichens occupy habitats at the centimeter scale, while vascular plants could be said to occupy habitats at the meter scale. In addition, lichens can grow in some microhabitats where vascular plants are not found, e.g., house roofs or rocks. However, when the range of natural areas was expanded to include those larger than 1000 km$^2$, a relationship between vascular plant and lichen floras was found. This is most likely due to the effect area has on increasing ecosystem diversity, which produces more overall habitat diversity and hence species diversity.

The similarity clusters of the parks based on the two types of floras were not completely congruent. Both separated Indiana Dunes and Cuyahoga Valley from the other seven parks, although St. Croix was grouped with them for the vascular plants. This separation of Cuyahoga Valley and Indiana Dunes is probably related to geographic distance, but may also be confounded by the profound effects of air pollutants on the lichen floras. In the remaining seven parks, Isle Royale appeared rather unique for lichens in this region, but not for vascular plants. In fact, for vascular plants, very little splitting of the cluster of seven was apparent (Bennett 1996b). Lichen floras in this area appeared to be more unique geographically than vascular plant floras, probably due to the diversity of species in the Great Lakes, not the distribution of species per se.

The ratio of six vascular plant species to one lichen species for North America appears to hold on average for the 33 areas as well (Table 6): the overall average ratio for these areas was 6.20 (SD = 5.89). The ratio found for the world floras, however, was an exception: it was over double the average ratio for North America. No logical explanation can be proposed at this time for this anomaly.

In conclusion, although average similarities of these nine parks, based on vascular plants and lichens, were comparable (just over 30%), this generalization hides the fact that the two types of floras do not appear related to one another at this scale. There was a closer relationship among the vascular plant floras than among the lichen floras, suggesting that geographic affinities between them are weaker for lichens. Thus, management strategies to conserve the vascular plant floras may not conserve the lichen floras on an equal basis. Lichen biodiversity may have to be managed differently than vascular plant biodiversity.

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RHODORA, Vol. 101, No. 907, pp. 298–299, 1999

## NEW ENGLAND NOTE

# NOTES ON THE HABITS AND LIFE-HISTORY OF *BIDENS DISCOIDEA*: AN EPIPHYTE IN MASSACHUSETTS FLOODPLAIN PONDS

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*Bidens discoidea* (T. & G.) Britton is uncommon or undercollected in Massachusetts and in need of attention from field botanists to clarify its status in the state (Sorrie 1990; P. Somers, pers. comm.). It resembles the common *B. frondosa* L. for which it is easily mistaken. However, the two species are readily identified in the field by the number of outer involucral bracts: three to five in *B. discoidea,* and five to ten in *B. frondosa.*

*Bidens discoidea* is an annual whose range covers much of the eastern half of the United States and adjacent Canada (Gleason and Cronquist 1991). Wiegand (1899) considered the species to be "quite rare in New England" and more common in the western part of its range where it grows on logs and stumps in lakes and bogs. In the southeastern Coastal Plain it is found "usually on fallen logs and stumps in swamps" (Fernald 1936) and is "conspicuous" in freshwater tidal swamps (Beaven and Oosting 1939).

Sorrie (1990) commented that he was aware of four extant Massachusetts stations for *Bidens discoidea* and noted habitats as ponds, oxbows, and buttonbush (*Cephalanthus occidentalis* L.) swamps. He also noted an occurrence of it growing as an epiphyte, but provided no further details. Robert Bertin (pers. comm.) recently found previously undocumented populations of *B. discoidea* on the shores of a cluster of beaver ponds in Worcester County, Massachusetts, most commonly growing on partially submerged stumps and logs, but occasionally on shoreline soils.

*Bidens discoidea* is common on floodplain ponds along the Nashua River on land now or formerly part of the Fort Devens Military Reservation in Worcester and Middlesex Counties, Massachusetts. Here, the species is found almost exclusively growing as an epiphyte on *Cephalanthus occidentalis* and was observed on 13 out of 15 floodplain ponds inventoried in 1995 and 1996. In these ponds, water levels typically decline a meter or more between spring and late summer, but levels fluctuate during the growing season in response to precipitation patterns (M. Hickler, unpubl. data). Shoreline vegetation in these ponds often includes dense thickets of *C. occidentalis.* At least three species of moss [*Climaceum americanum* Brid., *Drepanocladus aduncus* (Hedw.) Warnst. var. *kneiffi* (Schimp. in B.S.G.) Mönk., and *Dichelyma capillaceum* (With.) Myr.] grow on *Cephalanthus* stems, where they form dense tufts, concentrated around the normal high water mark.

*Bidens discoidea* has a strategy for avoiding the stresses associated with unpredictable hydrology and light competition from *Cephalanthus* in this habitat. The awned achenes, which are well adapted for dispersal by hitchhiking on passing animals, are also perfectly pre-adapted to lodge in the thick tufts of moss. Achenes germinate in their mossy seedbeds after water levels begin to recede in the spring but long before ground-level soil has drained. The roots then follow the receding water toward the ground (M. Hickler, pers. obs.). Perched high in the *Cephalanthus* stems, the aerial portions of the plants are above the influence of flooding and in position to penetrate through the dense *Cephalanthus* canopy to where there is ample sunlight. By late summer, *B. discoidea* plants can be seen throughout the *Cephalanthus* swamps with their tops above the shrub canopy in full sunlight and roots projecting down, sometimes a meter or more, to the soil.

ACKNOWLEDGMENTS. Thanks to Roberta Lombardi and Sarah Cooper-Ellis for moss identifications.

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## NEW ENGLAND NOTE

# A NEW BARNSTABLE COUNTY, MA, RECORD FOR *ASCLEPIAS PURPURASCENS*

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While inspecting the status of a small population of *Rhododendron canadense* (L.) Torr. present in a moist woodland habitat on the edge of a shallow wetland depression in Falmouth, Massachusetts, we discovered three individuals of *Asclepias purpurascens* L. (Asclepiadaceae) in the understory ground cover. The species is found from New Hampshire to Virginia, west to Iowa, Kansas, and Oklahoma, and north to Wisconsin (Gleason and Cronquist 1991). Purple milkweed is identified as belonging to a "Division 2; Regionally Rare Taxa" category in "*Flora Conservanda:* New England" by Brumback and Mehrhoff et al. (1996) with fewer than 20 current occurrences in New England. Purple milkweed is a State Threatened taxon in Massachusetts with two extant occurrences. In New Hampshire, Connecticut, and Rhode Island, purple milkweed is listed as a State Historic taxon with no extant populations. The taxon is not reported from Maine or Vermont. Previous records for *A. purpurascens* on Cape Cod and the Islands are rare with only a few occurrences documented during the past decade (P. Somers, Massachusetts Natural Heritage and Endangered Species Program, pers. comm.). A single specimen was collected in 1986 from a dry heathland community on the Miacomet Plains on Nantucket (Sorrie and Dunwiddle 1996). Two early records of *A. purpurascens* from dry oak forest habitat in West Tisbury and Chilmark are referenced in *The Flora of Martha's Vineyard* published by the Martha's Vineyard Sandplain Restoration Project (1998). Despite repeated surveys performed in conjunction with the New England Plant Conservation Program (NEPCoP) sponsored by the New England Wild Flower Society in Framingham, Massachusetts, the authors have been unable to relocate a Barnstable County population discovered by

Richard LeBlond in 1989 under a transmission line corridor in Brewster, Massachusetts. This species is not mentioned in "Notes on the rare flora of Massachusetts" (Sorrie 1987).

The Barnstable County plants were first observed on July 8, 1998. A single terminal umbel comprised of 24 flowers atop a pubescent peduncle was observed on the taller (50 cm height) specimen. The smaller specimens did not produce inflorescences. Distinguishing features included the bright magenta hoods (7 mm), which turned darker purple-red with age. The erect hoods clearly surpassed the gynostegium and the short, incurved horns. The opposite, elliptical leaves (15 cm) had distinct petioles, transverse veins and an acuminate leaf tip. The stem was slightly hairy while the undersurface of the leaf was covered with short, downy hairs. The upper surface of the leaf was glabrous.

Associated species in the ground cover included *Pyrola rotundifolia* L. var. *americana* (Sweet) Fern., *Gaultheria procumbens* L., *Vaccinium angustifolium* Aiton, and *Lycopodium obscurum* L. under an open canopy of *Pinus rigida* Miller, *Quercus alba* L., and *Q. velutina* Lam. A locally rare fern, *Osmunda claytoniana* L., occurred on the upland slope of the wetland depression intermixed with *O. cinnamomea* L.

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## NEW ENGLAND NOTE

# *CYPERUS MICROIRIA*: A NEW ADDITION TO THE FLORA OF CONNECTICUT

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*Cyperus microiria* Steudel (Cyperaceae). Hartford County: Windsor, Huckleberry Road, waste area at town landfill, moist acidic loamy fine sand, rare, 18 Sep 1998, *Zebryk 5760* (NEBC, EIU). Determined by Gordon C. Tucker, Eastern Illinois University.

While conducting a floristic inventory and rare plant survey at Northwest Park and vicinity for the Town of Windsor, Connecticut, an unusual *Cyperus* was noted among other ruderal species at the adjacent Windsor Town Landfill. Bearing a distinct resemblance to *C. iria* L., a somewhat invasive Eurasian species common throughout the southeastern U.S., this unknown specimen was determined to be *C. microiria*, an annual native to China, Korea, and Japan.

Apparently a rare adventive in eastern North America, *Cyperus microiria* has previously been reported in New York City, Philadelphia, and recently in Kentucky. The collection from Windsor is only the second known from New England (G. Tucker, pers. comm.), the first being from Wayland, Massachusetts (*P. Adakonis s.n.*, 13 Sep 1979, Wayland, Middlesex County; MASS).

The landfill at Windsor serves as a haven and probable point of dispersal for a large number of invasive introduced and native species, including *Cyperus esculentus* L., *Froelichia gracilis* (Hook.) Moq., *Setaria glauca* (L.) P. Beauv., *S. geniculata* (Lam.) P. Beauv., *S. viridis* (L.) P. Beauv., *Microstegium vimineum* (Trin.) A. Camus, and *Cirsium arvense* (L.) Scop. At the present time, little is known about the potential for *Cyperus microiria* to become a troublesome invasive weed, similar to *C. rotundus* L. in the South, or the widespread *C. esculentus*. Certainly the small population at Windsor, if it persists, is worth monitoring to evaluate the potential impact of this species in our region.

RHODORA, Vol. 101, No. 907, pp. 303–305, 1999

# BOOK REVIEW

*Proceedings of a Symposium on the Recovery and Future of the Northeastern Forest, Connecticut College, April 12, 1997* edited by Robert A. Askins and Glenn D. Dryer. 1998. Published in the journal *Northeastern Naturalist*, Volume 5, Number 2, pp. 95–172. ISSN 1092-6194 $10.00 (paperback). Published by collaborative effort based at the Humboldt Field Research Institute, Steuben, ME (available from http://maine.maine.edu/~eaglhill; mention this review and receive a 20% discount).

On April 12, 1997, the Center for Conservation Biology and Environmental Studies at Connecticut College, New London, sponsored a symposium for land managers, conservationists, and educators in environmental science, designed to assist in the determination of whether biological diversity and ecological functioning is restorable and sustainable. The seven presenters, a commendable ensemble of some of the more notable ecologists in the field today, have produced a symposium of papers which is both thoughtful and informative. The overall viewpoint is one of integrative ecology (the belief that complex systems such as ecosystems must be looked at as a whole, over long periods, to be understood), however the reductionist perspective is also represented, as well as suggestions from environmental economists.

The take-home message of this symposium is clearly that northeastern forests need to be evaluated and a balance struck between their ecological and subjective social value, and then proactively managed to foster and protect such states. The point that nature is dynamic and therefore there is no historical state which should serve as our restorative target, is often repeated. Lesser themes of the conference include the need for long-term research, the effects of air pollution on forest ecosystems, and the need to improve the processes by which ecological research is disseminated to managers and policy-makers. The conference admirably wrestles with the coexisting evidence of forests in metabolic decline, systemically speaking, while many forest species are on the increase.

William A. Niering provides a good start with his overview of the natural and anthropogenic agents affecting regional forests in his paper "Forces that shaped the forests of the northeastern United States." The impacts of human settlement, by far the predominant influence, is recounted from the Indian to the post-colonial period, and current threats such as pollution, introduction of exotic species, and fragmentation of forests are cited.

David R. Foster and Glenn Motzkin follow by asserting the importance of a historical perspective in the interpretation of forest landscapes for ecological conservation, management, and development in "Ecology and conservation in the cultural landscape of New England: Lessons from nature's history." The authors claim that while climate and elevation were the primary forces shaping regional forests in precolonial days, past land-use and edaphic factors exert the reigning influences on vegetative composition and structure today. They introduce the point that nature has no static ideal; vegetative communities have no record of long-term consistency, nor have regional floras shown any tendency to revert to floras of the past. Mankind thus has strongly influenced both past and future forest states.

Gene E. Likens and Kathleen F. Lambert discuss the critical need for sustained research in their paper "The importance of long-term data in addressing regional environmental issues." They strongly present the danger of using short-term data to evaluate long-term patterns, the need for safeguarding long-term data and research sites in perpetuity, and recommendations that experimental designs be adaptable to future concerns and not "question-driven." Also advocated is the use of long-term watershed ecosystem research to guide sustainable forestry policy.

John M. Skelly takes the road less traveled with his clearly reductionist perspective in "A brief assessment of forest health in northeastern United States and southeastern Canada." He argues that while air pollution may be a forest stressor, there has been no hard evidence that regional forests are in decline. In support of this view are cited two short-term and one ten-year forest agencies study, which found no clear cause-effect relationship between the tree mortality and pollution deposition.

In "The epidemiology of forest decline in eastern deciduous forests," Orie L. Loucks elegantly and effectively refutes the reductionist viewpoint. What begins as a discussion of the appropriate research framework for the study of complex systems ends in a well-presented scientific argument concluding that air pollution has indeed been the cause of large-scale tree mortality in the region. Along the way, the integrative versus reductionist approaches are discussed, and the systematic symptoms of "forest decline" are defined.

Dina Franceschi and James R. Kahn present the economist's perspective in "The potential contribution of economics to the recovery of northeastern forests." Their point is that the social benefits of healthy forests need to be determined, and then policies providing economic incentives to landowners and managers need to reflect these goals. As long as private benefits exceed the public good, forests will continue to be developed, fragmented, and polluted.

Lastly, John Kricher delivers a summary of sorts with "Nothing endures but change: Ecology's newly emerging paradigm," in which he states that human stewardship of natural systems is essential. The concept of "nature's balance" is a western philosophical construct which must be dismissed so that proactive goals for ecosystem management can be determined and achieved. Clearly, the northeastern forests of tomorrow are being shaped by the perspectives of land managers, conservationists, and educators of today. This symposium does a commendable job of representing these evolving perspectives.

—Leslie Teeling, Department of Plant Biology, University of New Hampshire, Durham, NH 03824.

RHODORA, Vol. 101, No. 907, pp. 306–308, 1999

## BOOK REVIEW

*Discovering the Unknown Landscape: A History of America's Wetlands* by Ann Vileisis. 1997. xii+433 pp. illustrations, photos, appendix, map, index. ISBN 1-55963-314-X $27.50 (cloth). Island Press, Washington, DC.

In the preface (p. xi–xii) of *Discovering the Unknown Landscape: A History of America's Wetlands*, author Ann Vileisis states that, "The matter of wetlands and their conservation is not a matter of science alone—but one of culture as well." Building upon this thesis, Vileisis examines the interactions between Americans and their neighboring wetlands from colonial to modern times. Throughout the narrative, readers learn how the 221 million acres of wetlands that were once distributed across America were systematically reduced to approximately 102.3 million acres by the 1990s. Efforts to develop and exploit wetland habitats as well as the more recent desire to conserve wetlands are examined within the prevailing political, economic, and environmental trends of American society. From the harvesting of salt marshes by New England colonists to the levee systems of the United States Army Corps of Engineers, readers learn how various attitudes and policies permanently altered the complexion of the continent.

Concepts of wetland science are frequently discussed in the text. However, the objective of the narrative is not to explain details of wetland biology and hydrology, but instead to chart the actions of society as the ecological values of wetlands became better understood. Throughout *Discovering the Unknown Landscape*, the complex interactions of government agencies, politicians, and private citizens are illustrated. The eighteen chapters have titles such as, "A Landscape on the Periphery," "Wetlands Portrayed and Envisioned," "Federal Bulldozers and Draglines," "The Reagan Agenda Challenges Wetland Gains," and "The Promise of Restoration." Each chapter is divided into several subtopics relating different aspects of the chapter theme. Regions that are revisited throughout the book include the Florida Everglades, the bottomland swamps of Louisiana, the riparian wetlands of the Mississippi drainage, the prairie potholes of the upper Great Plains, and the Central Valley of California. Some of the topics discussed include:

- the early perceptions of wetlands, including those of writers and artists
- the consequences of the Swamp Land Acts of the mid-1800s
- contradictory federal policies, some of which promoted wetland reclamation for agriculture and economic development, while other legislation encouraged wetland conservation
- the continued degradation of the nation's wetlands by a swelling post-World War II population, and the increasing efforts of conservationists at local, state, and federal levels
- the Federal Water Pollution Control Act of 1972 (the Clean Water Act) and the debate over the regulation of wetland development through the interpretation of Section 404
- the environmental impacts of the Reagan administration, the "no net loss" wetland directive of the Bush administration, and the policies of the Clinton administration as well as the 104th Congress

Vileisis has provided a thorough summation of an extensive and complex topic within American environmental history. The narrative is organized well and reads smoothly despite the abundance of agency acronyms and references to legislation that potentially could make prose cumbersome. As one decade sets the tone for the next, the reader gains an awareness of the historical precedents that have contributed to contemporary wetland issues.

*Discovering the Unknown Landscape* has been extensively researched. The 64 pages of notes organized by chapter are a useful resource. The notes contain a wealth of information cited from diverse sources ranging from technical government documents and academic histories to the popular press. A 12-page index, numerous archival photographs and illustrations, and the occasional map and graph also enhance the text.

The one page appendix entitled "Some Common and Scientific Names of Wetland Plants" consists of a wide spectrum of species with both cosmopolitan (e.g., *Phragmites australis* and *Typha latifolia*) and regional (e.g., *Avicennia germinans* and *Cladium jamaicense*) distribution patterns. Among this list of plant species there are some editorial problems, including a few misspellings such as *Lythrum salarica* [sic] and some taxonomic confusion. The scientific name *Scirpus acutus* includes the author citation when all other species have the author omitted. *Spartina pectinata* is placed in the list three times under various names; it is cited with the common names "black grass," "sloughgrass" (under the synonym *S. michauxiana*), and "prairie cordgrass." The common name prairie cordgrass was paired with the apparently non-existent scientific name *S. pectiana* (see Kartesz 1994). Regarding other common names, *Nymphaea odorata* is cited oddly as "water lily tuber," and "sheep laurel" (*Kalmia angustifolia*), is erroneously paired with the scientific name for mountain laurel (*K. latifolia*), an upland laurel species.

*Discovering the Unknown Landscape* has provided an important service by placing our scientific knowledge of wetland values within the framework of our nation's history. Vileisis (p. 350) concludes by stating that, "Informed by history, we can remember the trade-offs already made and turn away from the mistakes and misunderstandings of a time when we knew no better." This enhanced perspective is a valuable complement to the wetlands dialogue that too frequently finds human economics and development at odds with environmental concerns. While reading the story of our American wetlands it becomes painfully apparent that as a nation we have not really "discovered the unknown landscape." Instead, by using our technological and engineering prowess, we have attempted to conquer a vital feature of our natural topography that too often has been viewed as a blight rather than a blessing.

*Discovering the Unknown Landscape* is an informative addition to the literature of the history, politics, and public perceptions of American wetlands. At the conclusion of the first chapter, Vileisis (p. 10) observes that, "Perhaps a newfound awareness of wetlands can inspire and nourish a vision of stewardship for these long-abused and misunderstood landscapes." *Discovering the Unknown Landscape* contributes significantly to the ongoing effort to elevate the importance of wetlands in our nation's conscience. Readers will gain a clear appreciation for the issues that have defined the relationships between American culture and the wetlands that are finally beginning to be appreciated and better understood. For educators, conservationists, consultants, politicians, or any reader with a general interest in the history of American wetlands, *Discovering the Unknown Landscape* is a thought-provoking synthesis and a highly recommended resource.

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—C. ERIC HELLQUIST, 391 West Road, Adams, MA 01220.

RHODORA, Vol. 101, No. 907, pp. 309–310, 1999

## BOOK REVIEW

*Flora of Maine: A Manual for Identification of Native and Naturalized Vascular Plants of Maine* by Arthur Haines and Thomas F. Vining. 1998. 837 pp. with 10 blank, numbered pages for notes. ISBN 0-9664874-0-0 $45.00 plus shipping (paperback). V. F. Thomas Co., Bar Harbor, ME.

Botanists in Maine can claim a number of luminaries over the past two centuries. We begin with John Josselyn, who compiled the first list of plants observed in Scarborough in 1672. Merritt L. Fernald and his colleagues named our state botanical society in honor of Josselyn a few years before joining with others in Cambridge, Massachusetts, to create the New England Botanical Club. The authors of the recently published *Flora of Maine*, Arthur Haines and Thomas F. Vining, acknowledge a nearly unbroken thread of field-oriented catalogs and listings that have provided information for their work. This latest manual is the first (nearly) complete flora.

Two years and two months seem hardly enough time to produce a state flora, yet Haines and Vining have called on years of experience in the field, in university classrooms and laboratories, and amongst a large number of colleagues and advisors to produce a credible and accessible volume. It is an essential volume for the libraries of New England botanists and institutional libraries everywhere.

The most important element of a flora, for this reader, is its keys. Every manual treats a different segment of the plant world defined by a combination of factors, including political geography, topography, taxonomic group, or the particular interests and needs of readers. Haines and Vining have prepared keys to the vascular plants native or naturalized to Maine, and they warn that such a scope allows them to use characters for identification that might not be appropriate elsewhere. Nevertheless, the keys to families (following Judd et al. 1999) are sound and usable: well written, segmented into logical groups, and based on easily recognizable field characters.

Keys to genera and species comprise essential characters wherever possible. Complete descriptions of genera and species are not found here as they are in *Gray's Manual* (Fernald 1950) or the *Manual of Vascular Plants of Northeastern United States and*

*Adjacent Canada* (Gleason and Cronquist 1991). Yet the reader can easily build such complete descriptions from the information used to create the keys. Special notes appear for taxa that have a designated rank of rarity following the criteria of the Maine Natural Areas Program.

The *Flora of Maine* should certainly be found on the desk or in the satchel of Maine's resident and visiting botanists. It may be a model for botanists in neighboring New England states, and perhaps it will inspire the long-overdue revision of our most important regional flora, *Gray's Manual* (Fernald 1950). The University of Maine should be proud of the work of authors Arthur Haines and Tom Vining.

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JUDD, W. S., C. S. CAMPBELL, E. A. KELLOGG, AND P. S. STEVENS. 1999. Plant Systematics: A Phylogenetic Approach. Sinauer Associates, Inc., Sunderland, MA.

—W. DONALD HUDSON, JR., Chewonki Foundation, Wiscasset, ME 04578-4822.

RHODORA, Vol. 101, No. 907, pp. 311–317, 1999

# NEBC MEETING NEWS

**March 1999.** Thomas J. Rawinski, Director of Ecological Management at Massachusetts Audubon's Center for Biological Conservation, addressed the Club on the topic "Travels through Virginia: Botanical Wonders and Conservation Victories." It was a partial accounting of his seven years away from New England, or in his words, "a report back to the hive," regarding his employment as an ecologist with the Virginia Division of Natural Heritage, part of the state's Department of Conservation and Recreation. Using slide images and recounting many botanical discoveries and new natural areas protected as a result of the Division's efforts, he gave us an overview of the state's natural areas and botanically diverse ecosystems. He reminded us of how much M. L. Fernald had loved Virginia, noting that Fernald added more new species to his 8th edition of *Gray's Manual of Botany* from Virginia than from Newfoundland, another area he had explored extensively.

Contrasting Virginia with New England, Rawinski said Virginia has only two natural lakes, lacks some northern taxa such as *Chamaedaphne*, and is nearly devoid of paper and gray birch. As evidence of a richer flora than New England, he noted that there were 25 oaks, 8 pines, 6 magnolias, 25 *Rhynchospora* spp., 13 *Vaccinium* spp., and 10 *Trillium* spp., plus representation by families such as the Bromeliaceae and Loganiaceae. Virginia endemics include three species of *Clematis*: *C. addisonii*, which occurs on dolomite; *C. coactilis*, a species found on both dolomite and shale; and *C. viticaulis*, a narrow endemic found only on shale barrens. Other endemics include *Helenium virginicum*, a species of acid ponds in the Shenandoah Valley, and *Iliamna corei*, a species for which they found fire worked well as a management tool.

The clearly defined physiographic provinces of the state helped Rawinski orient us to the state's major geological and climatic regions and to the locations of unique habitats for plants within them. Elevations range from the 5700 ft. high Mt. Rogers in the Blue Ridge Mountains in southwestern Virginia to sea level where one can find extensive tidal marshes. He compared the Piedmont of Virginia to Worcester County, Massachusetts, pointing out that neither is diverse in habitat types, but that each possesses some interesting ones, such as those with diabase bedrock.

Botanical hot spots are clustered in habitats such as shale barrens, sea-level fens, and dolomite outcrops: types found primarily in the eastern or western parts of the state. Using habitat characteristics as primary indicators, he and colleagues located 30 new state records, such as *Carex arctata* and *Sporobolus heterolepis*, between 1990 and 1997. Recent funding of 11.5 million dollars through a bond bill has allowed the Department to add over 20 new natural areas to its preserve system.

Rawinski highlighted certain ecosystems. More than 500 potential shale barrens were identified by the Heritage Division; they typically occur on steep hillsides undercut by streams. An abundance of limestone in the Shenandoah Valley and elsewhere has resulted in some notable dolomitic cliffs and, in the southwestern corner of the state, some calcareous glades with taxa such as the newly described clover species, *Trifolium calcaricum*. Dolomite glades supported the globally rare *Echinacea laevigata*, which can be found growing in loamy, dolomitic soil with prairie taxa such as *Castilleja coccinea* and *Senecio plattensis*. A priority for protection in Rawinski's eyes was an ultramafic barren (i.e., a serpentine-like area with high magnesium levels) in the Piedmont supporting several disjunct and rare species. Buffalo Mountain, a monadnock in the Blue Ridge, supported a diversity of vegetation associations and herbaceous species, including nine rare species for the state. Rawinski postulated that the thin soil mantle and open glade habitat is maintained by a natural deficiency of clay, which facilitates lateral movement of water and washing of any deposited soil. Ultramafic fens are another botanical hot spot in Virginia, providing habitat for 20 state-listed rare species, including a state record discovery: *Tofieldia glutinosa*. A truly significant area in the Piedmont is Fort Pickett Military Reservation, where frequent fires have maintained a population of the very rare sumac, *Rhus michauxii*, it occupies hundreds of acres, making it by far the largest known population.

The Coastal Plain, as in New England, has many ponds, but in Virginia they are sinkhole depressions over 100,000 years old. Here one can find large overcup oaks, *Quercus lyrata*, and rare herbs such as *Carex joorii*, *Hottonia inflata*, *Sabatia campanulata*, and *Chelone cuthbertii*. In an especially dry year, ten new *Fimbristylis perpusilla* records showed up at pond sites. Other coastal plain communities of special interest are sand hills with longleaf pine, pocosins or shrub bogs, sea level fens, and cypresstupelo swamps, where Virginia big-eared bats can be found in cavities of the ancient trees.

For more information on Virginia natural areas and biota, Tom Rawinski advised seeking out the Virginia Department of Conservation and Recreation's web site.

**April 1999.** Michael Donoghue introduced the "NEBC 1999 Distinguished Speaker," Dr. Peter Raven, Director of the Missouri Botanical Garden. Accomplishments and qualities mentioned included (1) his ability to organize and galvanize people around ideas and visions, (2) his authorship of *The Biology of Plants*, (3) his collaborative research on the Onagraceae as a model for systematic botany, (4) his leadership in coordinating the Flora of China project, and (5) his leadership in conservation of biological diversity, including serving on the President's Commission on Science and Technology and co-authoring a paper entitled "Teaming with Life," a statement on the need and mechanisms for preserving biodiversity.

Dr. Raven addressed the topic, "Plant Conservation Globally and Locally." He explained that his approach would be to paint the broadest picture possible of the current crisis in biological conservation around the world and why the crisis exists. His main objective was to stimulate our thinking about these issues and invite a dialogue about strategies for combating the problem. Raven's broadest picture included a review of 3.8 billion years of biological evolution on the earth and the five major extinction events that have influenced its pathways to the present. The first three extinction events occurred when life was restricted to the marine world. He pointed out that terrestrial life began 430 million YBP, at a time equivalent to 90% of the way through the time-line of earth's existence. He emphasized the importance of cyanobacteria in making colonization of terrestrial habitats possible by changing the earth's atmosphere to an oxidizing one. The resulting increase in oxygen produced by their photosynthetic activities over 3 billion years made possible the production of a stratospheric ozone layer that allowed the ancestors of the four groups dominant on land at the present time (arthropods, fungi, terrestrial vertebrates, and plants) to colonize terrestrial habitats. The fourth great extinction event occurred at the end of the Permian, about 280 YBP, impacting the earth's first forests and early dinosaurs. In the following Mesozoic Era, dinosaurs and cycads flourished and angiosperms evolved, making life much more diverse than previously.

About 65 million YBP, at the end of the Cretaceous Period, the fifth great extinction occurred, presumably as the result of a large meteorite crashing into the earth off what is now the Yucatan Peninsula. The collision created an opaque cloud around the globe that impeded photosynthesis and, according to estimates by David Raup et al., eliminated two-thirds of terrestrial species in a short period of time. At that point, Raven estimated loosely that the number of eucaryotic organisms remaining may have numbered between 500,000–700,000. It took approximately ten million years for life to recover, and the resulting evolutionary pathways led to the evolution of most current groups of organisms. Today, according to a 1997 paper by Sir Robert May presented at the National Forum on Biodiversity at the National Academy of Sciences, the number of eucaryotic species can be estimated conservatively at about seven million. Of these, only about one in four has a valid name. In the tropics, the ratio is much less, around one in twenty. Even for the described species of organisms our knowledge is extremely limited; many are known only from a single specimen at the bottom of a museum vial. No one can give a plausible estimate of the number of procaryotic organisms. One gram of soil in a Norwegian beech forest is estimated to have 5,500 species of bacteria, more than the total number of species recognized formally from the entire world, and how these figures relate to other ecosystems around the world, or to the total number of bacterial species, is unknown. Even more poorly known, Raven says, is the multitude of relationships that mediate the flow of energy through the globe's ecosystems and other aspects of their functioning.

Bringing humans into the picture, Raven drew attention to our *Homo erectus* ancestors who migrated out of Africa and discovered fire-making, causing some low-scale disturbances approximately 1.5–2 million YBP. *Homo sapiens* appeared on earth about 200,000 YBP and arrived in the New World 14,000–16,000 YBP. The cultivation of crops began at about 10,000 YBP at a number of widely-scattered centers, when there may have been only several million people globally, a population equivalent to that of the Greater Boston area today. Agriculture allowed for a reliable food source, and by the time of Christ the earth's population had grown to around 120–150 million. By the Renaissance, it had grown to 0.5 billion, and by the time of Thomas Malthus, who speculated at the start of the Industrial Revolution that human populations would outstrip agriculture's ability to produce food, about 1 billion people were walking the earth. By 1950, our numbers had increased to 2.5 billion, and now 50 years later, the earth's population has reached nearly 6 billion, bringing even greater importance to questions of sustainability.

"Sustainability and biodiversity are two sides of a coin," Raven said. Can the human world sustain itself while maintaining global biological diversity? The results of the last 50 years are not encouraging. One-fourth of the world's topsoil has been lost and one-third of the world's forests have been destroyed since World War II. There has been a drastic increase in extinction rates. It is estimated that extinction rates have increased 100 × since the Renaissance and are 1000 × background rates, based on fossil records. The rates are accelerating, according to extinction models developed by Stuart Pimm et al. using island biogeography theory, and may reach 10,000 × in the next century. Over the next 25 years, they estimate that one-third of tropical organisms will become extinct or be on the way to extinction, and that by the end of the next century, three-fourths of all tropical organisms and two-thirds of the worldwide total will be gone or on the way to extinction. *Homo sapiens*, Raven says, is driving an extinction event comparable to the scope of the fifth major extinction event 65 million years ago. Nothing could be as damaging to the future of our species, primarily because of our direct dependency on other living organisms. The 350,000 species of photosynthetic organisms—plants, algae, and a few bacteria—are responsible for all productivity on earth, and human beings obtain all their food from plants directly and indirectly. Another anthropocentric reason for preserving biodiversity is that three-fourths of humanity depends directly on biodiversity, mostly plants, for its pharmacopoeia while the remaining quarter go to drug stores and derive such benefits indirectly. Why say the 21st century will be the "Age of Biology," Raven asks, if all of the organisms are going down the drain? Where will we get all of the organisms to create new products or to use in new sustainable systems, or for that matter to use in bio-engineering new biological products or life forms? He cautions us to heed Aldo Leopold's advice and follow the "first rule of intelligent tinkering" by "saving all of the cogs and wheels."

Raven asks, "What things are in the way of fixing the problem?" One is the sovereignty and pride of nations that inhibit our ability to pay attention to one another internationally and establish global solutions. He cites the United States' failure to sign the "International Convention on Biological Diversity" as a prime example. A second appears to be greed and waste by the developed world, because Raven described the industrialized nations as possessing 20% of the world's population and 85% of the world's wealth, while creating 80–90% of its pollution. In the world today, 360 billionaires have wealth equal to what two billion of the poorest people earn in a year. The people at the low end of the economic spectrum are totally disenfranchised, which denies the rest of the world the potential benefit of their wisdom and creativity. We simplify when we say "over-population" is the problem globally. For instance, Brazil and Mexico have had population control policies for 20 years and have slowed population growth and improved education for women, whereas the U.S. has no population policy, despite a doubling of its population in the past 50 years and a standard of living 30–40 times that of Brazil or Indonesia. Because of our consumptive standard of living, the impact on the environment of doubling the U.S. population (adding 135 million people in 50 years) is equivalent to adding 4 billion people to populations in Brazil or Indonesia.

We do not need to waste at the levels we do. The United States wastes twice as much per capita as in Europe. We are living as if there is no tomorrow and in denial that our economy is related to the rest of the world. What can we do to help create a more sustainable world and slow the loss of biological diversity? Raven's answers include: (1) be leaders in showing the way rather than demanding that the third world lead the way, (2) pay attention to internationalism by convincing others that the 80% of the world's people living in non-industrialized countries are of deep and profound importance to us, (3) vote and encourage others to do so, (4) support conservation groups you are congenial with philosophically and then support sustainability, and (5) think about what you are doing personally and make wise choices. Raven says, "Think about what is just, what is stable, what is sustainable. Think about a world within which biological diversity, cultural diversity, beauty, music, poetry, philosophy, literature, and all the things we value and cherish can coexist. What do we do to create a world that will maintain these things?" We can be optimistic or pessimistic amidst the "gloom and doom" that we face. "Yes, the world will become more homogeneous and less diverse," Raven acknowledges. But the future depends on how we live now, he says. "If you want to be optimistic, do so because of your own determination to do something about it," says our 1999 Distinguished Speaker, as he leads the Club forward into its second century.

—PAUL SOMERS, Recording Secretary

# ANNOUNCEMENT

## NEW ENGLAND BOTANICAL CLUB GRADUATE STUDENT RESEARCH AWARD

The New England Botanical Club will offer $2,000 in support of botanical research to be conducted by graduate students in 2000. This award is made annually to stimulate and encourage botanical research on the New England flora, and to make possible visits to the New England region by those who would not otherwise be able to do so. It is anticipated that two awards will be given, although the actual number and amount of awards will depend on the proposals received.

The award will be given to the graduate student submitting the best research proposal dealing with systematic botany, biosystematics, plant ecology, or plant conservation biology. Papers based on the research funded must acknowledge the NEBC's support. Submission of manuscripts to the Club's journal, *Rhodora*, is strongly encouraged.

Applicants must submit three copies of each of the following: a proposal of no more than three double-spaced pages, a budget, and a curriculum vitae. Two letters in support of the proposed research, one from the student's thesis advisor, should be sent directly to the Awards Committee by sponsors. All materials should be sent to: Awards Committee, The New England Botanical Club, 22 Divinity Avenue, Cambridge, MA 02138-2020. Proposals and supporting letters must be received no later than March 1, 2000. The recipient(s) will be notified by April 30, 2000.

Two Graduate Student Research Awards were given in 1999. Joel Gerwin of the University of Massachusetts at Boston received support for his proposal entitled "Long-term effects of forest fragmentation on genetic diversity of red oak (*Quercus rubra* L.): A comparison of old-growth and secondary forests." Also chosen for an award was Julie Ellis of Brown University, whose proposal was entitled "The role of nesting seabirds in structuring New England coastal plant communities."

## ANNOUNCEMENT

## HUMBOLDT FIELD RESEARCH INSTITUTE PRIZE

The New England Botanical Club is offering a prize for the best essay of 500 words or fewer on the theme "How I would benefit from an Eagle Hill Seminar." This prize is offered in conjunction with the Humboldt Field Research Institute, and consists of tuition for a week-long Eagle Hill Field Seminar or Workshop in Steuben, Maine. In return for a donation from the Club of a set of *Rhodora* back-issues, the Institute has reciprocated with the donation to the Club of this prize. The contest is open to any member of the NEBC. Please submit three copies of your essay before December 31, 1999. Essays should be mailed to: The New England Botanical Club, ATTN: Eagle Hill Essay, 22 Divinity Avenue, Cambridge, MA 02138. The winner will be notified in advance and announced at the March, 2000, Annual Meeting.

# INFORMATION FOR CONTRIBUTORS TO RHODORA

Submission of a manuscript implies it is not being considered for publication simultaneously elsewhere, either in whole or in part.

GENERAL: Manuscripts should be submitted in triplicate. The text must be double-spaced throughout, including tables, figure legends, and literature citations. Use a non-proportional font throughout and do not justify the right margin. Do not indicate the style of type through the use of capitals, underscoring, or bold, except for names of genera and species which should be in italics or underscored throughout. Do not underline punctuation. All pages should be numbered in the upper right-hand corner. For guidance in matters not addressed here, consult the editorial office by phone at (603) 862-3205, FAX (603) 862-4757, or e-mail: janets@christa.unh.edu. Brevity is urged for all submissions. Submit manuscripts to the Editor-in-Chief.

TITLE, AUTHOR(S), AND ADDRESS(ES): Center title, in capital letters. Omit authors of scientific names. Below title, include author(s) name(s), affiliation(s), and address(es). If "current address" is different, it should follow immediately below, not as a footnote.

ABSTRACT: An abstract and a list of key words should be included with each paper, except for shorter papers submitted as Notes. An abstract must be one paragraph, and should not include literature citations or taxonomic authorities. Please be concise, while including information about the paper's intent, materials and methods, results, and significance of findings.

TEXT: Main headings are all capital letters and centered on one line. Examples are: MATERIALS AND METHODS, RESULTS, and DISCUSSION. Do not title the Introduction. Do not combine sections of the paper (such as Results and Discussion), or use Conclusions or Summary. Second level headings should be indented, bold, upper and lower case, and end with a period. Taxonomic authorities should be cited for all species names at their first usage in the text, or in a referenced table. Cite each figure and table in the text in numerical order. Each reference cited in the text must be in the Literature Cited. Cross-check spelling of author(s) name(s) and dates of publication. Literature citations in the text should be as follows: Hill (1982) or (Hill 1982). For two or more authors, cite as follows: Angelo and Boufford (1996) or (Angelo and Boufford 1996). Cite several references alphabetically by first author, rather than chronologically. Within parentheses, use a semicolon to separate different types of citations (Hill 1982; Angelo and Boufford 1996) or (Figure 4; Table 2).

FLORAS AND TAXONOMIC TREATMENTS: Specimen citation should be selected critically, especially for common species of broad

distribution. Keys and synonymy for systematic revisions should be prepared in the style of "A Monograph of the Genus *Malvastrum*," S. R. Hill, RHODORA 84: 159–264, 1982. Designation of a new taxon should carry a Latin diagnosis (rather than a full Latin description), which sets forth succinctly how the new taxon differs from its congeners.

LITERATURE CITED: All bibliographic entries must be cited in the paper, unless a special exception has been made by the Editor (such papers will be allowed a REFERENCES section). Verify all entries against original sources, paying special attention to spelling and details of publication. Cite references in strict alphabetical order by first author's surname. Do not write authors' names in all capital letters. References by a single author precede multi-authored works of same senior author, regardless of date. Use a long dash when the author(s) is the same as in the entry immediately preceding (see recent issues). Refer to Botanico-Periodicum-Huntianum (B-P-H 1968) and B-P-H/Supplement (1991) for standardized abbreviations for journals.

TABLES: Tables must be double-spaced. Tables may be continued on an extra page, if necessary. As much as possible, the title should be self-explanatory. Do not use footnotes; instead, add notes after the end of the table title. Broadside tables should be avoided, if possible. Each table should be cited in the text in numerical order.

FIGURES: Illustrations must be either black and white half-tones (photographs), drawings, or graphs. Illustrations must be camera-ready; flaws cannot be corrected by the Editor or the printer. Add symbols or shading with press-on sheets. The printed plate will be 4 × 6 inches; be sure that illustrations are proportioned to reduce correctly. Allow space for a caption, if possible. Magnification/reduction values should be calculated to reflect the actual printed size. Maps must indicate scale and compass direction. The double-spaced list of legends for figures should be provided on a separate page. Each figure should be cited in the text in numerical order.

# THE NEW ENGLAND BOTANICAL CLUB

22 Divinity Avenue
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The New England Botanical Club is a nonprofit organization that promotes the study of plants of North America, especially the flora of New England and adjacent areas. The Club holds regular meetings, and has a large herbarium of New England plants and a library. It publishes a quarterly journal, RHODORA, which is now in its 101st year and contains about 400 pages per volume. Visit our web site at http://www.herbaria.harvard.edu/nebc/

Membership is open to all persons interested in systematics and field botany. Annual dues are $35.00, including a subscription to RHODORA. Members living within about 200 miles of Boston receive notices of the Club meetings.

To join, please fill out this membership application and send with enclosed dues to the above address.

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